Check List the journal of biodiversity data

ANNOTATED LIST OF SPECIES

Check List 18 (2): 289–321
https://doi.org/10.15560/18.2.289

PENSOFT.

An updated herpetofaunal species inventory of Iona National Park in southwestern Angola

Javier Lobón-Rovira[1,2,3*], Pedro Vaz Pinto[1,3,4,5], François S. Becker[6], Krystal A. Tolley[7,8], John Measey[9], Bruce Bennet[10], Bastiaan Boon[10], Sango de Sá[10,11], Werner Conradie[12,13]

1 Centro de Investigação em Biodiversidade e Recursos Genéticos (CIBIO), InBIO Laboratório Associado, Campus de Vairão, Universidade do Porto, Vairão, Portugal • JLR: j.lobon.rovira@cibio.up.pt https://orcid.org/0000-0003-4380-9427 • PVP: p.vazpinto@cibio.up.pt

2 Departamento de Biologia, Faculdade de Ciências, Universidade do Porto, Porto, Portugal

3 BIOPOLIS Program in Genomics, Biodiversity and Land Planning, CIBIO, Campus de Vairão, Vairão, Portugal

4 Fundação Kissama, Lar do Patriota, Luanda, Angola

5 TwinLab CIBIO/ISCED, Instituto Superior de Ciências da Educação da Huíla, Lubango, Angola

6 National Museum of Namibia, Windhoek, Namibia • phrogbecker@gmail.com https://orcid.org/0000-0003-3874-9183

7 South African National Biodiversity Institute, Kirstenbosch Research Centre, Cape Town, South Africa • k.tolley@sanbi.org.za https://orcid.org/0000-0002-7778-1963

8 Centre for Ecological Genomics and Wildlife Conservation, University of Johannesburg, Johannesburg, South Africa

9 Centre for Invasion Biology, Department of Botany and Zoology, Stellenbosch University, Stellenbosch, Western Cape, South Africa • jmeasey@sun.ac.za https://orcid.org/0000-0001-9939-7615

10 African Parks, Johannesburg, South Africa

11 Instituto Nacional da Biodiversidade e Conservação (INBC), Ministério da Cultura, Turismo e Ambiente da República de Angola, Luanda, Angola

12 Port Elizabeth Museum (Bayworld), Humewood, South Africa • werner@bayworld.co.za https://orcid.org/0000-0003-0805-9683

13 Department of Nature Conservation Management, Natural Resource Science and Management Cluster, Faculty of Science, George Campus, Nelson Mandela University, George, South Africa

* Corresponding author

Abstract

Angola has experienced an incredible increase of the knowledge of its herpetofauna over the past decade. However, accurate biodiversity inventories remain deficient for certain regions of particular conservation interest. We therefore provide an updated checklist of Iona National Park's herpetofauna, with 75 recorded species, including five amphibians and 70 reptiles, 40 of these recorded for the first time in Iona National Park. These species comprise ~80% of the reptile diversity of Namibe Province. Therefore, this work recognises Iona National Park as the most reptile-diverse protected area in Angola and is potentially one of the richest in southern Africa. Consequently, this work enhances the importance of specific conservation plans in the area and the need for further investigation into the hidden biodiversity of this region.

Keywords

Amphibians, biodiversity, checklist, conservation, molecular, reptiles

Academic editor: Ross MacCulloch | Received 9 November 2021 | Accepted 11 March 2022 | Published 1 April 2022

Citation: Lobón-Rovira J, Vaz Pinto P, Becker FS, Tolley KA, Measey J, Bennet B, Boon B, Sá S, Conradie W (2022) An updated herpetofaunal species inventory of Iona National Park in southwestern Angola. Check List 18 (2): 289–321. https://doi.org/10.15560/18.2.289

©The authors. This is an open access article distributed under the terms of the Creative Commons Attribution License (CC BY 4.0), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

Introduction

With a resurgence of Angolan herpetological research in the last decade, there has been a remarkable increase in knowledge of the herpetofauna, with the addition of numerous new country occurrence records (Branch and Conradie 2013; Conradie and Bourquin 2013; Ernst et al. 2014, 2015; Branch et al. 2019a; Conradie et al. 2020a), the rediscovery of species (Vaz Pinto et al. 2019; Baptista et al. 2020), and the description of 33 new species (Conradie et al. 2012a, 2012b, 2013, 2020b; Stanley et al. 2016; Ceríaco et al. 2018a, 2020a, 2020b, 2020c, 2021; Marques et al. 2019a, 2019b, 2020, 2022; Branch et al. 2019b, 2021; Hallerman et al. 2020; Nielsen et al. 2020; Lobon-Rovira et al. 2021; Parrinha et al. 2021; Baptista et al. 2021; Wagner et al. 2021). This renaissance of knowledge came about only after the improvement in political and social stability that followed more than two decades of civil war (Huntley and Ferrand 2019). Little scientific exploration prior to this period resulted in a significant lack of foundational information and has left many regions unexplored. In order to address these shortcomings, national inventories have been published to help summarise all the historical materials from Angola (Branch 2018; Marques et al. 2018; Baptista et al. 2019b; Branch et al. 2019c) and have set the foundation for future herpetological work. Several formal conservation areas, including national parks and reserves, have been the focus of herpetological surveys in the last decade (Ceríaco et al. 2014, 2016a, 2018b; Conradie et al. 2016, 2021; Butler et al. 2019; Baptista et al. 2019a; Ernst et al. 2020). The rapid improvement of our knowledge of Angolan herpetofauna, especially the number of new species descriptions, highlights the need to re-evaluate estimates of biodiversity richness across the country (Baptista et al. 2019a).

Iona National Park (hereafter Iona NP) is located in south-western Angola and is one of the largest protected areas in the country (Fig. 1A). Its biodiversity importance is well recognized internationally, and as a result it was incorporated into the Iona-Skeleton Coast Transfrontier Conservation Area—one of the largest transboundary conservation areas in Africa (Mason et al. 2020), comprising a diverse array of desert landscapes across a dramatic topographic gradient. Numerous herpetologists have visited the region in recent years, and this has led to the description of five new species from the park and immediate surroundings (Haacke 2008; Conradie et al. 2012b; Branch et al. 2021; Parrinha et al. 2021) and the documentation of several range restricted species, such as *Pachydactylus scutatus* Hewitt 1927, *P. rangei* (Andersson, 1908), *P. vanzyli* (Steyn & Haacke, 1966), and *Lygodactylus lawrencei* Hewitt 1927. To date, 37 herpetofaunal species (within four amphibian and 15 reptile genera) are documented to occur in extreme southwestern Angola including both Iona NP and surrounds, which includes the Namibe Partial Reserve to the north (Ceríaco et al. 2016a). More broadly, 14 species of amphibians and over 95 species of terrestrial reptiles have been recorded for the entirety of Namibe Province (Marques et al. 2018), which includes Iona NP. The entire province covers a fairly large area and is heterogeneous for vegetation, substrate, and topography, whereas Iona NP is characterised by a desert biome. While these broader geographic checklists of species are available, a concise herpetological checklist for Iona NP has never been published.

In this paper, we provide the results of numerous recent expeditions which have added greatly to the knowledge of species distributions, habitat, and taxonomy within the Iona NP and surrounding areas. A comprehensive species inventory for Iona NP is key to conserving its unique biodiversity, against the backdrop of massive global biodiversity loss (Faith and Walker 2002; Salerno et al. 2021). We summarize all previous herpetofaunal knowledge from Iona NP and report on records collected from four recent unpublished surveys. We also include historical materials from the Transvaal Museum (TM) collected by Wulf Haacke and Charles Koch between the early 1950s to late 1970s from Iona NP that have never been published. We update taxonomic changes to provide the most up to date species inventory and highlight some species groups for further systematic revision. This summary of knowledge can be used to inform national and international policy regarding the regional biodiversity.

Study Area

Iona NP was established as a Game Reserve in 1937 and elevated to National Park status in 1957 (Ministério do Ambiente 2018). The park covers approximately 15,150 km^2 and is located in southwestern Angola, in Namibe Province, south of 15.75°S. The park is bounded by the Southern Atlantic Ocean to the west and the Cunene River to the south, while the Curoca River drainage and a few mountain ridges form the northern and eastern boundaries (Fig. 1A). The local climate is greatly influenced by the cold Benguela upwelling, which has shaped the evolution of the Namib Desert (Huntley 2019). Ecological zoning defined four main zones in Iona NP, namely from west to east (from the coast moving inland): a narrow belt of coastal dunes and beaches under a permanent South Atlantic Ocean influence (here referred to as coastal desert); a sand sea formed by continuous dunes, ~45 km wide in the northwest narrowing to <10 km toward the Cunene River mouth in the south (here referred to as dunes sea); an extensive gravel and sand plain interspersed with rocky outcrops and dry valleys (here referred to as central plain); mountains and steep escarpment ridges in the easternmost region (here referred to as mountain region) (Fig. 2). The topography ranges from sea level in the west to elevations greater than 2000 m above sea level (a.s.l.) at the highest peaks in the east. The habitats are varied, ranging from very sparse vegetation and bushes in the drier western areas

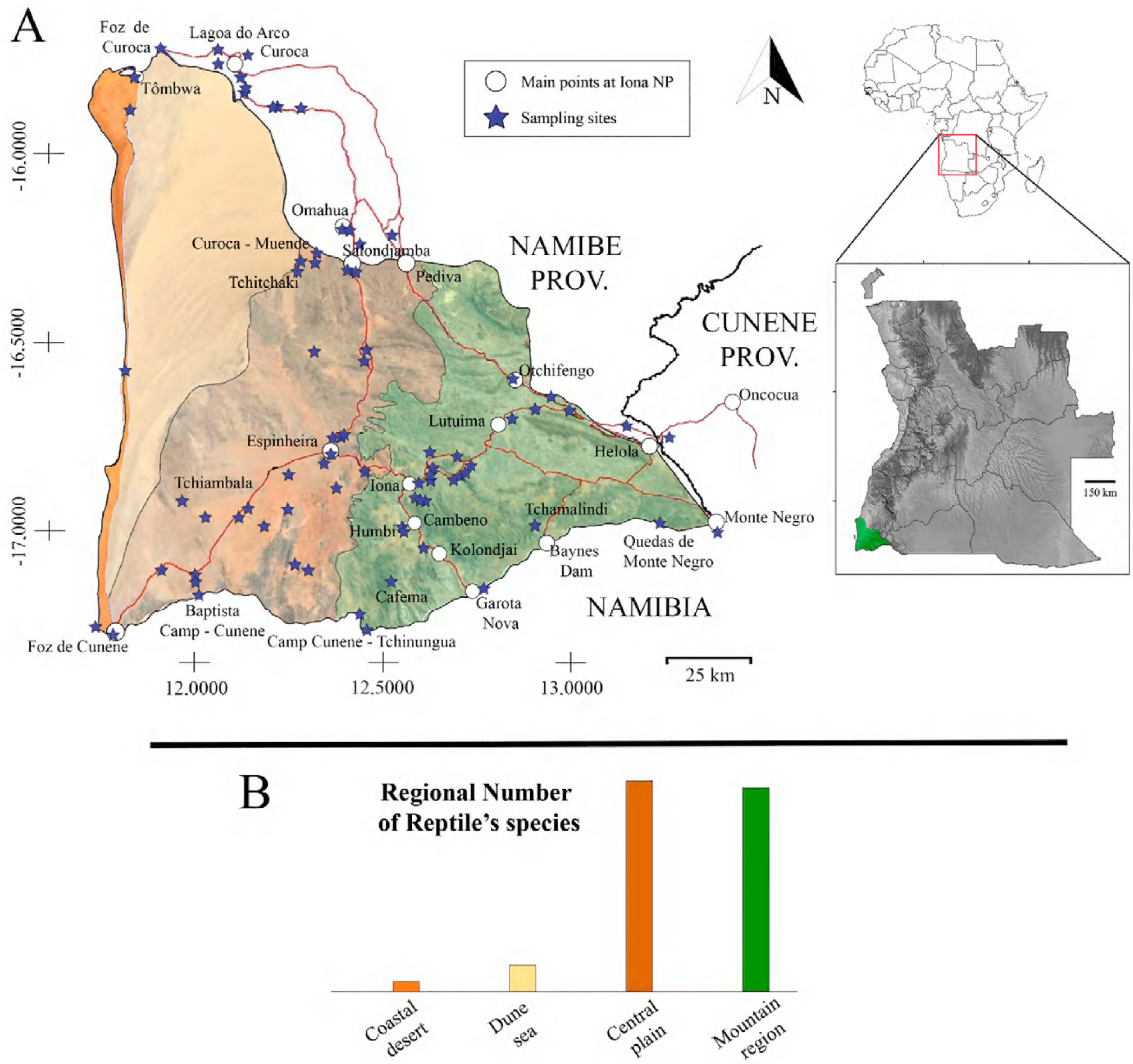

Figure 1. A. Map of Iona National Park highlighting the four main ecological zones within the park (orange: coastal desert; cream: dunes sea; light brown: central gravel and sandy plains; green: mountain region) superimposed over a digital elevation layer (darker shades indicate higher elevations). White circles depict the main reference points within Iona NP and surroundings. Stars depict localities where material has been collected. Red lines depict main access routes. **B.** Regional number of reptile species per main ecological zone of Iona NP.

that are abundant in succulent plants and also features the iconic *Welwitschia mirabilis* Hooker 1863, to spiny savanna and mopane woodlands in the eastern regions. The heterogeneous geography and habitats of this arid region contribute to the remarkable herpetological diversity present in the park.

The main study area is bounded by the formal boundaries of Iona NP, but we also included a buffer zone of 10 km to the north and east. This allowed the inclusion of records from fairly densely sampled areas outside the park but close to the park boundary from habitats that are contiguous with the park. Records from more than 10 km from the park boundary or from neighbouring Namibia were not included in our summary.

Methods

Sampling. The new material included in this summary was collected during four major herpetological expeditions conducted from 2009–2021, supplemented with shorter opportunistic visits to the park during this same period. The first expedition was carried out in January 2009 as part of the Angolan Biodiversity Assessment and Capacity Building Project. During that expedition, the team visited the plateau of Humpata and nearby escarpment and the coastal regions from Moçâmedes south to Foz do Cunene, including Iona NP. Three additional expeditions were carried out between March and August of 2021. In March 2021, the team surveyed

Figure 2. Examples of habitat diversity in Iona National Park. **A.** Fairy circles on sandy central plains. **B.** Small granitic icebergs on sandy central plains, **C.** Northern edge of dunes at Muende (Curoca River). **D.** Western mixed gravel and sandy plains. **E.** Espinheira plains. **F.** Western edge of dunes at Tchitchaki River. **G.** Curoca River. **H.** Vegetation patches on coastal dunes. **I.** Red mobile dunes on central plain. **J.** Omauha lodge. **K.** Saludjamba. **L.** Humbi (riverine mopane forest). **M.** Southern edge of dunes (rock valleys). **N.** Kolodjani (conglomerate formation). **O.** Between Iona and Lutuima (schists formations). **P.** Cafema. **Q.** Tchamalindi. R**.** Cunene River. Photographs by JLR (A–O), PVP (P, Q), and Octavio Mateus (R).

most regions of the park with the exception of the western highlands. During this survey, five different sites were surveyed between two and three days at each (Fig. 1A). The second expedition (May 2021) took place on or near the summits of two of the highest mountains in Iona NP, Serra Cafema and Tchamalindi. The elevational range surveyed was 1400–1750 m a.s.l. on Tchamalindi and 1850–2050 m. a.s.l. at Serra Cafema. A third expedition was conducted in August 2021, specifically focusing on remote sites not previously surveyed and targeting unreported species or taxonomically challenging taxa (Fig. 1A). Opportunistic data were also collected during and in between surveys, mostly since 2019. Photographs were taken of most species observed and tissue samples or vouchers were collected from some specimens that may represent new species or may constitute significant geographical range extensions.

Consequently, more than 50 sampling sites have been visited within Iona NP and 15 more in the surrounding 10 km buffer zone. Geographic coordinates were recorded for every record using the WGS84 system. Historical records often lack precise location data and except in cases where the collecting data is too vague, we here provide approximate coordinates, but refrain from adding elevation. Tissues samples were stored in 99% ethanol, and vouchers were fixed in 10% formalin or 96% ethanol and then transferred to 70% ethanol for long-term storage at Port Elizabeth Museum (PEM), South Africa or Colecção Herpetologica do Lubango (CHL) and Fundação Kissama (FKH), Angola. Where possible the breeding calls of amphibians were recorded with Ronald r-07 Handheld Recorder, and sonograms were obtained and processed with Raven v. 1.6.1 (The Cornell Lab of Ornithology, available at https://ravensoundsoftware.com). All amphibian calls recorded have been deposited in FonoZoo (http://www.fonozoo.com) at Museo Nacional de Ciencias Naturales, Spain.

Species identification. Individuals recorded from Iona NP were identified to species level based on external morphological characters detailed in published guides (Branch 1998; du Preez and Carruthers 2017; Channing and Rödel 2019; Chippaux and Jackson 2019). For identifications that were uncertain using only morphological features, a DNA barcoding and/or phylogenetic approach was used to aid in the identification (described below). For records that were based only on sight observations (including undocumented "catch and release"), the best estimate of identification was made in the field, and in cases of uncertainty these records were flagged as either "cf." (to be compared with), "aff." (similar to) or "sp." (not known), following (Sigovini et al. 2016).

In addition to these new survey data, distributional information from existing herpetological records were retrieved from the literature (Ceríaco et al. 2016a; Branch et al. 2017; Marques et al. 2018; Baptista et al. 2019; Marques et al. 2020; Branch et al. 2019). After consolidation of new and existing records, all new records were examined to assess whether they represented extensions to the known range.

DNA sequencing. We generated 16S rRNA sequences for those specimens where species level identification could not be confirmed using morphological traits. Total genomic DNA was extracted using EasySpin Genomic DNA Tissue Kit, following the manufacturer's protocols. The two genes were amplified using PCR with the following primers (16Sa and 16Sb; Palumbi et al. 1991). The PCR reactions were carried out in 10 µl volumes containing 1.5 µl of 25 ng/µl genomic DNA, 5 µl QIAGEN PCR MasterMix, and 0.4 µM of each primer. Thermal cycling was run with initial denaturation for 15 min at 95 °C followed by: 40 cycles with denaturation for 30 s at 95 °C, annealing for 35 s at 52 °C, extension for 45 s at 72 °C, and final extension for 10 min at 60 °C. PCR products were run on a 1% agarose gel and visualized under a UV light to verify amplification. Amplicons were sequenced using the forward primers on an ABI 3130xl Genetic Analyzer (Applied Biosystems, Foster City, California, USA) at Centre for Molecular Analysis (CTM, CIBIO–InBio). All sequences were checked and edited using GENEIOUS Prime v. 2021.1.1 (http://www.geneious.com) and aligned using the MUSCLE plugin for GENEIOUS. To aid in species level identificaiton, sequences were compared to the nucleotide database available in GenBank using the BLAST algorithm (https://blast.ncbi.nlm.nih.gov/Blast.cgi; Altschul et al. 1997), with the *nblast* default parameters. This retrieved the most similar homologous sequences available in the online database. Once identifications had been made, intraspecific variation was assessed through estimates of uncorrected pairwise sequence distance (*p*-distance) for 16S in MEGA v. 10.1.7 (Table S2). All sequences have been deposited in GenBank, and the accession numbers are provided in the species accounts below.

Results

We recorded a total of 75 species, representing five amphibian and 70 reptile species (five testudines, one crocodile, 48 lizards, 16 snakes; Table 1). Records occurred across all four of the main ecological zones within the park (Fig. 1A), although most species were recorded from the central plains (40 spp.) and eastern mountains (37 spp.), compared to the dune sea (5 spp.) and coastal desert (2 spp.) (Table 1; Fig. 1B). However, some species, such as amphibians, marine turtles, crocodiles, or water monitors could not be associated with any of these ecogical zones because of their aquatic habits (Table 1). Although most of the species were collected during the four main surveys, seven species (*Phrynobatrachus natalensis* (Smith, 1849), *Stygmochelis pardalis* (Bell, 1828), *Pelomedusa subrufa* (Bonnaterre, 1789), *Rhoptropus afer* Peter, 1869, *Typhlacontias johnsonii* Andersson, 1916, *Psammophis leopardinus* Bocage, 1887, *Psammophis trigrammus* Günther, 1865) have only been confirmed for

Tables 1. Species which have been recorded from Iona National Park and the 10-km buffer zone around the park, including localitites [tabulated according to the four main ecological zones coded as follows: CD (coastal desert), DS (dune sea), CP (central plains) and MR (mountain region)] and dates, including information from previous reports [codes listed below read as follow: OV (opportunistic visits) and HS (historical surveys and literature). "x" denotes reptile and amphibian species recorded from that ecological zone or survey, while "N/A" denotes species that were not included in any zone because their aquatic habitat.

Order	Family	**Scientific name**	Ecological zone				Surveys from present study				Other recent surveys		Other sources
			CD	DS	CP	MR	Jan-09	Mar-21	May-21	Aug-21	OV	Ceríaco et al. 2016	HS
Amphibia	Bufonidae	*Sclerophrys pusilla*	N/A	N/A	N/A	N/A				x			
	Pyxicephalidae	*Tomopterna tuberculosa*	N/A	N/A	N/A	N/A				x			
		Tomopterna ahli	N/A	N/A	N/A	N/A	x	x				x	
	Microhylidae	*Phrynomantis annectens*	N/A	N/A	N/A	N/A	x	x				x	
	Phrynobatrachidae	*Phrynobatrachus natalensis*	N/A	N/A	N/A	N/A							x
Testudines	Cheloniidae	*Chelonia mydas*	N/A	N/A	N/A	N/A					x		
		Lepidochelys olivacea	N/A	N/A	N/A	N/A					x		
	Trionychidae	*Trionyx triunguis*	N/A	N/A	N/A	N/A					x		x
	Testudinidae	*Stygmochelis pardalis*	N/A	N/A	N/A	N/A							x
	Pelomedusidae	*Pelomedusa subrufa*	N/A	N/A	N/A	N/A							x
Crocodylia	Crocodylidae	*Crocodylus niloticus*	N/A	N/A	N/A	N/A					x		
Squamata	Gekkonidae	*Afroedura donvae*				x	x	x					
		Condrodactylus laevigatus			x			x					
		Condrodactylus fitzsimonsi			x	x	x	x	x	x	x	x	
		Condrodactylus pulitzerae			x		x	x	x	x	x	x	
		Hemidactylus benguellensis			x				x	x	x		
		Kolekanos plumicaudus			x	x	x	x	x		x	x	x
		Lygodactylus lawrencei			x	x		x					
		Lygodactylus nyanyeka			x	x		x	x	x	x		
		Pachydactylus caraculicus				x		x					
		Pachydactylus cf. *oreophilus* complex				x		x	x	x	x	x	
		Pachydactylus cf. *punctatus* complex			x	x	x	x	x	x	x	x	
		Pachydactylus parascutatus			x				x	x			
		Pachydactylus rangei	x	x				x		x			x
		Pachydactylus rugosus				x				x			
		Pachydactylus scutatus		x	x			x		x		x	x
		Pachydactylus vanzyli			x		x	x		x			x
		Rhoptropus barnardi			x	x	x	x	x	x		x	
		Rhoptropus biporosus			x	x	x	x	x	x	x	x	x
		Rhoptropus boultoni			x	x	x	x	x	x	x	x	x
		Rhoptropus afer			x								x
		Rhoptropus sp.			x			x				x	
	Lacertidae	*Meroles anchietae*		x			x	x			x	x	x
		Meroles reticulatus	x				x	x			x	x	x
		Pedioplanis serodioi			x		x	x					
		Pedioplanis haackei			x		x	x				x	
		Pedioplanis huntleyi				x	x	x	x				
	Cordylidae	*Cordylus namakuiyus*				x			x				
	Gerrhosauridae	*Cordylosaurus subtessellatus*			x			x				x	
		Gerrhosaurus skoogi		x				x				x	
		Matobosaurus maltzahni				x		x					
	Scincidae	*Panaspis mocamedensis*				x			x				
		Trachylepis acutilabris			x		x	x	x	x	x	x	x
		Trachylepis sp.				x		x					x
		Trachylepis binotata			x	x			x				
		Trachylepis hoeschi			x				x				
		Trachylepis occidentalis			x			x				x	
		Trachylepis cf. *chimbana*				x		x	x			x	
		Trachylepis laevis			x	x	x	x					x
		Trachylepis punctulata			x		x	x				x	x
		Trachylepis sulcata				x		x	x			x	x
		Typhlacontias punctatissimus bogerti			x		x	x				x	
		Typhlacontias johnstoni		x									x

Order	Family	Scientific name	Ecological zone				Surveys from present study				Other recent surveys		Other sources
			CD	DS	CP	MR	Jan-09	Mar-21	May-21	Aug-21	OV	Ceríaco et al. 2016	HS
Squamata	Varanidae	*Varanus albigularis angolensis*			x	x		x					
		Varanus niloticus	N/A	N/A	N/A	N/A						x	x
	Chamaeleonidae	*Chamaeleo dilepis*				x	x						
		Chamaeleo namaquensis			x		x	x					
	Agamidae	*Agama anchietae*			x	x	x	x				x	x
		Agama planiceps			x	x	x	x	x	x	x	x	x
	Pythonidae	*Python anchietae*			x			x					
		Python natalensis			x	x		x					
	Viperidae	*Bitis arietans*			x	x			x	x			
		Bitis caudalis			x			x		x		x	x
	Psammophiidae	*Psammophis namibiensis*		x				x					x
		Psammophis notosticus			x			x				x	
		Psammophis leopardinus				x							x
		Psammophis trigrammus				x							x
		Hemirhagerrhis viperina				x			x				
	Lamprophiidae	*Lycophidion namibianum*			x		x						
	Prosymiidae	*Prosymna* cf. *frontalis*			x		x						
		Prosymna visseri			x		x						
	Pseudaspididae	*Pythonodipsas carinata*			x			x		x			
	Elapidae	*Naja nigricincta*			x						x		x
	Leptotyphlopidae	*Namibiana* cf. *occidentalis*			x						x		

Iona NP based on historical materials and previous bibliography records (Table 1).

Below we provide a brief summary of each species' distribution, identification, biology, and material available. Other new surveys not listed above (since 2010) are cited where relevant, but those materials are not listed here as they are listed in their respective published works. Ditsong Museum of Natural History (formerly TM) material is listed here because it was not included in previous works. Museum accession numbers for material collected are given for each species as follow: PEM = Port Elizabeth Museum, TM = Ditsong Museum of Natural History, FKH = Fundação Kissama. For other codes (tissue samples) listed below, see Table S1.

Amphibia

Bufonidae

***Sclerophrys pusilla* (Mertens, 1937)**

Figure 3A

Material examined. ANGOLA – **Namibe Province** • Quedas do Montenegro; −16.9968, 013.2480; 596 m a.s.l.; FKH 0673, FKH 0674; GenBank: ON006587, ON006588.

Identification. *Sclerophrys pusilla* is a large toad (SVL 80 mm) with flattened parotid glands, sharp snout profile, and the absence of any red markings on the posterior surface of the legs (du Preez and Carruthers 2017). The morphological identifion was confirmed genetically. DNA sequences of these specimens are very similar (~0.2% 16S *p*-distance) to a previously sequenced specimen of *S. pusilla* from Cacuchi River, Angola (GenBank accession: KT862862).

Biology and distribution. This species is often associated with shallow, static, or slow-moving rivers with variety of vegetation types in lowveld grassland and savannas of Sub-Saharan Africa (du Preez and Carruthers 2017). In Angola, the species is widely distributed (Marques et al. 2018); however, it had not been recorded previously from Iona NP.

Pyxicephalidae

***Tomopterna ahli* (Deckert, 1938)**

Figure 3B

Material examined. ANGOLA – **Namibe Province** • Humbe Valley; −16.9996, 012.5443; 876 m a.s.l.; 2♂ and 1♀, FKH 0821–0823; GenBank: ON006589, ON006590 • Caiyonona Spring; −16.9079, 012.5787; 899 m a.s.l.; 6 Metamorphs, PEM A09157, PEM A09159–63.

Identification. Moderate size frog (SVL ~35.6 mm), with robust body and short head. Dorsal pattern consists of green or brown blotches with black and golden warts on pale beige background. Many *Tomopterna* species are very difficult to identify morphologically and thus we rely on genetics and calls for proper identification. Specimens from Humbe were identified genetically and are very similar (<1% 16S *p*-distance) to a previously published record from Namibia (GenBank accession: MN104601) (Table S2). *Tomopterna damarana* was until recently considered to be part of the *T. cryptotis* (Boulenger, 1907) complex; however, a recent taxonomic revision showed that *T. ahli* is in fact, a senior synonym of *T. damarana* (Channing and Becker 2019).

Biology and distribution. *Tomopterna ahli* is a medium-sized (SVL 35 mm) sand frog that is associated with arid woodlands and savanna (du Preez and Carruthers 2017 as *T. damarana*). This species had been reported along the borders of Iona NP at Pediva springs (Ceríaco et

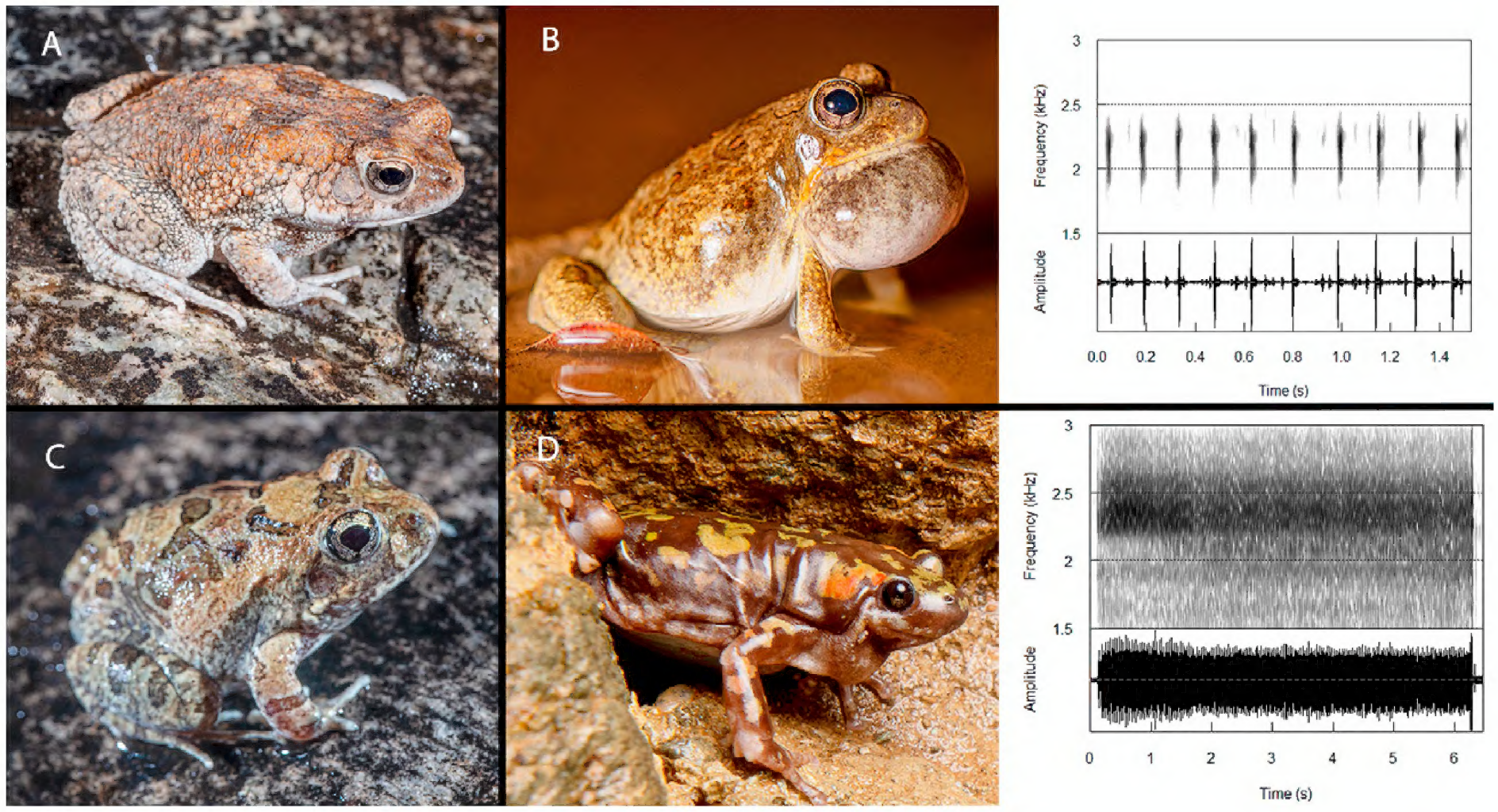

Figure 3. Amphibians from Iona National Park, with sonograms of breeding calls where available. **A.** *Sclerophrys pusilla*. **B.** *Tomopterna ahli* (graphic sonogram). **C.** *Tomopterna tuberculosa*. **D.** *Phrynomantis annectens* (graphic sonogram). Photographs by PVP (A, C) and JLR (B, D).

al. 2016a) and at Epupa Falls, Namibia (Heinicke et al. 2017). Some individuals were found actively calling or in amplexus in the evening after a rainstorm created temporary pools in semi-open areas among acacias and succulent plants (*Cyphostemma uter*, *Aloe* spp.) in the lower part of the westernmost mountains of the park between granitic and conglomerate formations (Fig. 2N). The call presents a dominant frequency of 2128 Hz and basal frequency ~1073 Hz (upper harmonics are multiples of this). Single notes are emitted continuously at a note repetition rate of ~6.4 notes/s, note duration 8–9 ms (SOUNDCODE: FZ12969, Fig. 3A). However, when compared with topotypic recordings, our vocalization recording differs slightly, with shorter, more distinct notes, a lower dominant frequency, and a slower note rate (Channing and Becker 2019).

***Tomopterna tuberculosa* (Deckert, 1938)**
Figure 3C

Material examined. ANGOLA – **Namibe Province** • Quedas do Montenegro; −16.9968, 013.2480; 596 m a.s.l.; 1♂, FKH 0675; GenBank: ON006591.

Identification. Large frog (SVL ~45 mm). Dorsum rough with skin ridges and near symmetric dark markings with narrow white borders. The specimen reported here is genetically identical to specimens previously collected by Hayes et al. (unpubl. data) in Malanje Province, Angola (GenBank accession: MK036492).

Biology and distribution. *Tomopterna tuberculosa* is a fossorial species widely distributed across highland savannas in southern Africa (du Preez and Carruthers 2017). In Angola, the species occurs mainly in highland savannas associated with rocky substrate, reaching the lowlands in the semi-arid savannas of Kwanza Sul and Benguela provinces (Marques et al. 2018). However, in Namibe Province this amphibian had been reported from only Bibala (Bocage 1895) and the bottom of Leba Pass (Poynton and Haacke 1993). Here, we document a specimen collected at Quedas do Montenegro (= Epupa Falls, Angola). This record is the first of this species from within Iona NP and represents the southernmost record for Angola.

Microhylidae

***Phrynomantis annectens* (Werner, 1910)**
Figure 3D

Material examined. ANGOLA – **Namibe Province** • Caiyonona Spring; −16.9079, 012.5787; 899 m a.s.l.; Tadpoles, PEM A13330 • Mupaka River; −16.8584, 012.6759; 819 m a.s.l.; FKH 0824–8; GenBank: ON006592–ON006595.

Identification. Adults (SVL 40 mm) were identified morphologically, based on the typical, yellow-spotted coloration of *P. annectens*, with marked red flanks on the head in males, while tadpoles were identified by its characteristic dark dorsal coloration with scattered golden flecks and a golden stripe extending from body along upper edge of tail muscles (du Preez and Carruthers 2017). DNA barcoding of specimens collected at Mukapa River exhibit a low divergence to one another (0.32%) and also low compared to unpublished sequences originated from Benguela Province (<1%; Baptista et al. unpubl. data 2021; Table S2).

Biology and distribution. *Phrynomantis annectens* occurs in arid regions from western Angola, through Namibia to north-western regions of South Africa (du Preez and Carruthers 2017). This species was previously

recorded from Omauha Lodge in the vicinity of Iona NP (Ceríaco et al. 2016a). During the March 2021 survey, more than 40 individuals were observed calling during an explosive breeding event after rain. The calling males were located on the edge of temporary streams in valleys crossing the mountainous region between Iona and Lutuima villages. The call is reminiscent of a jackhammer, with a series of rapid pulses issued at a rate of ~114.6 pulses per second, call duration ~6 seconds (600–700 pulses per call), with an inter-call interval ~5–10 s. Dominant frequency was 2292 Hz (SOUND-CODE: FZ 12970, Fig. 3B).

Phrynobatrachidae

***Phrynobatrachus natalensis* (Smith, 1849)**

Material examined. ANGOLA – **Namibe Province** • Foz do Cunene; −17.2600, 011.7900; TM 40693; historical material.

Identification. This species is characterized by a stout body (SVL 40 mm) with small head and pointed snout with close-set eyes (du Preez and Carruthers 2017). Recent studies have demonstrated that *P. natalensis* encompasses several cryptic species (Zimkus et al. 2010; Bittencourt-Silva 2019). Until fresh material can be collected and applied to the re-evaluation of the species complex, we consider the existing material as part of the *P. natalensis* complex.

Biology and distribution. *Phrynobatrachus natalensis* is widely distributed across western, eastern, and southern Africa, commonly associated with permanent or temporary water bodies (Channing and Rödel 2019). To date, the species has only been collected once in Iona NP at Foz do Cunene (Poynton and Haacke 1993).

Reptilia
Testudines
Chelonia

***Chelonia mydas* (Linnaeus, 1758)**
Figure 4A

Material examined. ANGOLA – **Namibe Province** • Foz do Cunene; −17.2638, 011.7949; 0 m a.s.l.; photographic records.

Identification. The species is a medium-sized sea turtle (carapace straight-length 900–1100 mm), characterised by four non-overlapping costal scutes on each side of the shell, and only a single pair of large scales on top of its head, between the eyes and nostril (Spotila 2004).

Biology and distribution. This worldwide distributed species is commonly observed at the mouth of the Cunene River (Foz do Cunene) where great numbers of individuals are known to aggregate to feed. Recent surveys have reported over 300 sightings in one single transect (Morais 2021). This species is commonly observed along the Angolan coast with occasional breeding, but nesting has never been documented along the coast of Iona NP (M. Morais pers. comm. 2021).

***Lepidochelys olivacea* (Eschscholtz, 1829)**
Figure 4B

Material examined. ANGOLA – **Namibe Province** • Ponta Albina; −15.8922, 011.7320; 0 m a.s.l.; photographic record.

Identification. This species is the smallest sea turtle (carapace straight-length 600–700 mm), and nearly circular carapace with 6–9 costal scutes (Spotila 2004).

Biology and distribution. *Lepidochelys olivacea* is the most abundant species of sea turtle along the Angolan coastline, and its nesting population possibly consists of one of the largest "non-arribadas" (i.e., solitary nesting turtles) worldwide (M. Morais pers. comm. 2021). Although more abundant in central and northern Angola, it is known to regularly breed successfully in Iona NP just south of Ponta Albina, in what constitutes the southernmost nesting locality for the species in the eastern Atlantic (Morais 2021).

Figure 4. Reptiles in the families Agamidae, Varanidae, Chamaeleonidae, and Testudines from Iona National Park. **A.** *Chelonia mydas*. **B.** *Lepidochelys olivacea*. **C.** *Tryonix triungis*. **D.** *Chamaeleo namaquensis* (juvenile). **E.** *Chamaeleo dilepis*. **F.** *Agama anchietae*. **G.** *Agama planiceps*. **H.** *Varanus albigularis angolensis*. Photographs by Alvaro Baptista (H), William R. Branch I, Michel Morais (B, C), JLR (D, F–G), and PVP (A).

Trionychidae

***Trionyx triunguis* (Forsskål, 1775)**
Figure 4C

Material examined. ANGOLA – **Namibe Province** • Foz do Cunene; −17.2600, 011.7900; TM 41312–3; historical material • Foz do Cunene; −17.2446, 011.7512; 0 m a.s.l.; photographic record.

Identification. This species is the largest soft-shell terrapin in Africa (carapace straight-length 500–800 mm), characterized by absence of flexible flaps over the hind limbs (Branch 1998).

Biology and distribution. This species is found in most of the major African rivers from the Nile to South Africa (Branch 1998, 2008; Rhodin et al. 2017). *Trionyx triunguis* has been reported as common all along the Cunene River (Griffin and Channing 1991; Simmons et al. 1993; Cunningham et al. 2018).

Testudinidae

***Stigmochelys pardalis* (Bell, 1828)**

Material examined. ANGOLA – **Namibe Province** • Iona 20 km W from Oncócua; −16.7400, 013.2500; TM 40767; historical material.

Identification. This species is a medium-sized to large tortoise (shell straight-length 300–500 mm), characterised by its domed but not hinged carapace (Branch 1998, 2008).

Biology and distribution. *Stigmochelys pardalis* is widely distributed across southern and eastern Africa, reaching its northern limit in Ethiopia or Sudan (Branch 1998, 2008; Rhodin et al. 2017). However, in Angola a few scattered records have been reported in literature from Benguela, Namibe, Cunene and Cuando-Cubango provinces (Conradie et al. 2016; Marques et al. 2018), but none from Iona NP. We note that one historical specimen here mentioned was collected during Charles Koch's expedition to Iona NP in 1963 and deposited in the Transvaal Museum, which seems to have been previously overlooked.

Pelomedusidae

***Pelomedusa subrufa* (Bonnaterre, 1789)**

Material examined. ANGOLA – **Namibe Province** • Iona 15 km W from Oncócua; −16.7100, 013.2900; TM 40788; historical material • Iona 38 km W from Oncócua; −16.7200, 013.1200; TM 40769; Historical material.

Identification. A medium-sized, side-necked terrapin (shell straight-length 150–200 mm) with a flat, hard, thin shell with no plastral hinge (Branch 1998, 2008).

Biology and distribution. This species is widely distributed in southern Africa (Branch 1998, 2008; Rhodin et al. 2017). It is often associated with large waterbodies and probably occurs along the Cunene River.

Crocodilia
Crocodylidae

***Crocodylus niloticus* Laurenti, 1768**

Material examined. ANGOLA – **Namibe Province** • Foz do Cunene; −17.2638, 011.7949; 0 m a.s.l.; photographic record.

Identification. The Nile Crocodile is the only representative of the family in southern Africa. They are large animals that may exceed 1000 kg in weight (Branch 1998). The jaws are long and have prominent teeth. The eyes and valved nostrils are situated on top of the head. The skin is covered with geometrically arranged, horny plates, many of which are keeled and bony. The hind feet are webbed.

Biology and distribution. *Crocodylus niloticus* is widely distributed across Africa, historically occurring in most major rivers across its distribution. It is commonly recorded along the Cunene River (Griffin and Channing 1991; Simmons et al. 1993; Cunningham et al. 2018).

Squamata
Chamaeleonidae

***Chamaeleo namaquensis* Smith, 1831**
Figure 4D

Material examined. ANGOLA – **Namibe Province** • 13 km SW from Espinheira; −16.8422, 012.2507; 520 m a.s.l.; FKH 0796; GenBank: ON006596 • 30 km SW from Espinheira; −16.9799, 012.1849; 595 m a.s.l.; PEM R17935; GenBank: HQ130516.

Identification. A large (SVL 120–140 mm), ungainly chameleon with a robust head and large mouth. DNA sequencing for FKH 0796 indicated that it was identical for 16S to a previously published sequence from Angola (PEM R17935, GenBank accession: HQ130516; Table S2) and identical to material collected from Namibia (GenBank accession: AY217950).

Biology and distribution. This species occurs in arid regions from South Africa, throughout Namibia and into southwestern Angola (Tilbury 2018). There is only one historical published record from Angola (Marques et al. 2018), although park rangers at Iona NP claim that this species is commonly observed during the rainy season. The two new records provided here are the only recently collected material from Angola. One specimen (PEM R17935) was collected moving within a "fairy circle" (Fig. 2A), while the second specimen (FKH 0796) was found digging in sand under a *Welwitschia miriabilis* on a gravel plain near Espinheira (Fig. 2E).

***Chamaeleo dilepis* Leach, 1819**
Figure 4E

Material examined. ANGOLA – **Namibe Province** • Iona Mountain; −16.9164, 012.5996; 1633 m a.s.l.; PEM R17982; GenBank: OK584789.

Identification. The specimen reported here was identified genetically. However, phylogenetic analyses have shown that *C. dilepis* probably contains several cryptic species. The Iona Mountain specimen belongs to a clade that includes material from southern and south-central Africa, whereas *C. dilepis* from northern and central Angola nests in a clade that includes material from central Africa (Main et al. in review). Given that the type locality of *C. dilepis* is coastal Gabon, it is likely to fall within the central African clade. Therefore, in the event of taxonomic changes, the southern African clade that includes the Iona locality would not retain the name *C. dilepis*.

Biology and distribution. This species occurs across most of Sub-Saharan Africa. *Chamaeleo dilepis* is the most widespread chameleon across Angola, being present on the plateau, escarpment, and coastal lowlands (Marques et al. 2018). However, this specimen is the only reported record for Iona NP, collected during the 2009 survey.

Gekkonidae

***Afroedura donveae* Branch, Schmitz, Lobón-Rovira, Baptista, Antonio & Conradie, 2021**
Figure 5A

Material examined. ANGOLA – **Namibe Province** • Omauha Logde; −16.2006, 012.4018; 341 m a.s.l.; PEM R17936, R17937, PEM R18041, R18042; GenBank: LM993776, LM 993777.

Identification. *Afroedura donveae* is a dorsoventrally flattened gecko (SVL 49.1–55.7 mm) with dark eyes and bright yellow dorsal bands (Branch et al. 2021). DNA sequence divergence was low amongst the individuals we collected (Table S2).

Biology and distribution. This is a rock-dwelling species commonly associated with large granitic boulders (Fig. 2J) with overhanging trees or medium-sized bushes that they frequently climb onto at night to hunt. During the day, individuals can be found hiding in rock crevices.

Figure 5. Species of the family Gekkonidae from Iona National Park. **A.** *Afroedura donvae*. **B.** *Chondrodactylus fitzsimonsi*. **C.** *Chondrodactylus laevigatus*. **D.** *Chondrodactylus pulitzerae*. **E.** *Hemidactylus benguellensis*. **F.** *Kolekanos plumicaudus*. **G.** *Lygodactylus lawrencei*. **H.** *Lygodactylus nyaneka*. **I.** *Pachydactylus caraculicus*. **J.** *Pachydactylus* cf. *oreophilus*. **K.** *Pachydactylus parascutatus*. **L.** *Pachydactylus* cf. *punctatus* complex. **M.** *Pachydactylus rangei*. **N.** *Pachydactylus* cf. *rugosus*. **O.** *Pachydactylus scutatus*. **P.** *Pachydactylus vanzyli*. **Q.** *Rhoptropus barnardi*. **R.** *Rhoptropus biporosus*. **S.** *Rhoptropus boultoni*. **T.** *Rhoptropus* sp. Photographs by JLR (A–D, F–J, L, P, Q, S, T) and PVP (E, K, M–O, R).

This Angolan endemic was recently described from just north of Iona NP (Branch et al. 2021) and has not yet been confirmed within the park boundaries. However, given the proximity (~8 km) to the park border of these records and the presence of continuous suitable habitat in northern Iona NP, we consider the species as likely to be present and expect it to be recorded in the future.

***Chondrodactylus fitzsimonsi* (Loveridge, 1947)**
Figure 5B

Material examined. ANGOLA – **Namibe Province** • Mongo; −17.0398, 012.6010; 917 m a.s.l.; FKH 0800, FKH 0810; GenBank: ON006597, ON006598 • Manaculama; −16.8193, 012.7188; 793 m a.s.l.; FKH 0816; GenBank: ON006599 • Tchamalindi; −16.9756, 012.8856; 1436 m a.s.l.; P1.106, P1.108; GenBank: ON006600 • Serra Cafema; −17.1269, 012.5126; 2033 m a.s.l.; P1.119; GenBank: ON006601 • Mupaka camp; −16.8433, 012.6888; 847 m a.s.l.; P1.269; GenBank: ON006602.

Identification. *Chondrodactylus fitzsimonsi* is a large gecko (SVL ≥ 89.3 mm) that can be distinguished from closely related species by the presence of smooth and partially rounded dorsal tubercles, versus dorsal keeled turbercles. The lowland specimens differ from the highland specimens by ~3% (16S; Table S2) and <3.5% from material collected from Epupa Falls, Namibia (GenBank accession: AF449109).

Biology and distribution. This species is a ground-dwelling gekkonid widely distributed across Namibe Province, including southwestern Angola and adjacent Namibia (Bauer and Lamb 2005; Ceriaco et al. 2016b; Marques et al. 2018). In Iona NP it is typically found in broken terrain near granitic (Fig. 2N) or schist formations (Fig. 2O). Interestingly, the species was more common in the highlands than the lowlands of Iona NP, with several specimens observed at Mount Tchamalindi and Cafema.

***Chondrodactylus laevigatus* (Fischer, 1888)**
Figure 5C

Material examined. ANGOLA – **Namibe Province** • Uaua; −16.8453, 012.6135; 819 m a.s.l.; JLRZC0138; GenBank: ON006603.

Identification. *Chondrodactylus laevigatus* is a large gecko (SVL ≥ 100 mm) that could be confused with its sister species *C. pulitzerae*; however, it is characterised by the lack of two vertebral rows of reduced scales from neck to sacrum. Head and body somewhat depressed, and dorsum with distinctly raised, but keelless or very weakly keeled tubercles (Heinz et al. 2021). Furthermore, DNA barcoding shows that this species differs from other Angolan *Chondrodactylus* species between 9.4 and 14.6% (*C. fitzsimonsi* and *C. pulitzerae*, respectively; Table S3).

Biology and distribution. The species was described from Karas Region in southern Namibia, where it is frequently recorded but has been subsequently documented from several regions in Angola (Schmidt 1933; Monrad 1937; Hellmich 1957; Conradie et al. 2016; Marques et al. 2018). Recent published material has also recovered this species from Moçamedes (Heinz et al. 2021), and our new record adds to the known records in Angola and the first within Iona NP. One individual was found at night on a granitic boulder north of Iona village.

***Chondrodactylus pulitzerae* (Schmidt, 1933)**
Figure 5D

Material examined. ANGOLA – **Namibe Province** • Guelengue; −16.9591, 012.0359; 469 m a.s.l.; JLRZC0125, GenBank: ON006604 • Humbi; −16.9853, 012.5419; 871 m a.s.l.; FKH 0817 • Espinheira; −16.7885, 012.3583; 456 m a.s.l.; PEM R17957.

Identification. This is a large, thick-toed gecko (SVL ≥102 mm) characterized by rows of large keeled dorsal tubercles separated by two middorsal rows of reduced scales. Sequence divergence has shown that *C. pulitzerae* differs <1% from other specimens collected from northern Namibe Province (J. Lobón-Rovira et al. unpubl. data 2020).

Biology and distribution. *Chondrodactylus pulitzerae* is the most widespread and abundant *Chondrodactylus* species in Angola, occurring in western Angola from Luanda to Namibe provinces and is also present in the central and northern plateau (Marques et al. 2018). The species is often found at night moving across open areas (Fig. 2A, E, G), among boulders of varying sizes (Fig. 2D, 2J). The species was previously reported to be widely distributed across Iona NP (Ceríaco et al. 2016a). It has been observed in syntopy with either *C. fitzsimonsi* (at Iona Highlands) or *C. laevigatus* (at Uaua).

***Hemidactylus benguellensis* (Bocage 1893)**
Figure 5E

Material examined. ANGOLA – **Namibe Province** • Tchinhungua; −17.2257, 012.4369; 249 m a.s.l.; FKH 0609–10; GenBank: ON006605, ON006606 • Lutuima–Muinde road; −16.8363, 012.6983; 845 m a.s.l.; FKH 0615–6; GenBank: ON006607 • Muende River; −16.5212, 012.3140; 317 m a.s.l; FKH 0564, FKH 05645; GenBank: ON006608, ON006609 • Lagoa do Arco; −15.7644, 012.0644; 51 m a.s.l; FKH0354; GenBank: ON006610.

Identification. This is the most variable *Hemidactylus* in size (SVL 37–60 mm) in Angola and the only species of this group present in southern Angola. It can be distinguished from other species of the *H. benguellensis*-group (Lobon-Rovira et al. 2021) based on the presence of rows of keeled dorsal tubercles, a large number of precloacal-femoral rows, and a large number of supralabilals (Lobon-Rovira et al. 2021). DNA barcoding shows that divergence within this species for samples collected from Angola is 0.42% (Table S2).

Biology and distribution. *Hemidactylus benguellensis* is an arboreal species and one of the most widely

distributed Angolan *Hemidactylus*. Lobón-Rovira et al. (2021) reported one specimen from Lagoa do Arco, within the buffer zone of this study, and four specimens at Muinde, ~30 km north of Espinheira in the central plains of Iona NP. The later were the first records of *Hemidactylus* within Iona NP, and the south-westernmost records for the genus in Angola. Subsequently, we recorded the species in two additional localities in the park, including the banks of the Cunene River. These new records fill the gap between Angolan and northern Namibia records reported by Ceriaco et al. (2020a).

***Kolekanos plumicaudus* (Haacke, 2008)**
Figure 5F

Material examined. ANGOLA – **Namibe Province** • Omauha Lodge; −16.1987, 012.4012; 339 m a.s.l.; FKH 0782; GenBank: ON006611 • 7 km north of Iona; −16.8583, 012.6127; 808 m a.s.l.; PEM R18010–R18014 • Tchamalindi; −16.9756, 012.8831; 1459 m a.s.l.; FKH 0574; GenBank: ON006612 • Serra Cafema; −17.1269, 012.5126; 2033 m a.s.l.; P1.126–7; GenBank: ON006613, ON006614 • Chiunge; −15.6857, 012.6131; 428 m a.s.l.; P1.75; GenBank: ON006615.

Identification. *Kolekanos plumicaudus* (SVL 37–45 mm) is the only leaf-toed gecko with feathered-tail ornamentation. Uncorrected net *p*-distances for 16S for samples collected across its known distribution are lower than 3.5% (Table S2). There seems to be some genetic structure between the lower and higher elevation populations.

Biology and distribution. Prior to our surveys, this species had only been recorded from a few localities in the granitic lowlands of the park and surroundings (Haacke 2008; Agarwal et al. 2017; Marques et al. 2018). Our surveys have extended the known range, which now covers several ecological zones and an elevation range of 70–2040 m a.s.l. (Vaz Pinto et al. 2021). This species can be observed at night moving among small, thin branches close to rock boulders. During the day it retreats into narrow cracks under rock flakes or into cracks in boulders.

***Lygodactylus lawrencei* Hewitt, 1926**
Figure 5G

Material examined. ANGOLA – **Namibe Province** • Humbi; −16.9853, 012.5419; 890 m a.s.l.; FKH 0811, 0812; GenBank: ON006616.

Identification. *Lygodactylus lawrencei* is a diurnal dwarf gecko (maximum SVL 28.8) that may be distinguished from similar and sympatric congeners by the presence of two cloacal pores (in males) and black chevron markings on the gular region and black ocelli above forelimbs (Marques et al. 2020). Genetically, these samples differ by ~2.5% for 16S from previously published material collected from Sesfontein, Namibia (GenBank accession: GU593428).

Biology and distribution. The species was described from the Kunene Region in northern Namibia, and some authors have predicted it to be present in Angola (Marques et al. 2018). Recently, a few specimens have been collected from Maungo and near Espinheira in Iona NP (Marques et al. 2020). In our surveys, we recorded this species from Humbi (Figs. 1, 3E), ~30 km southeast of Espinheira. This is presumably the most arid adapted species of the Angolan *Lygodactylus* and was recorded inhabiting large mopane trees along dry riverbeds (Fig. 2G). Individuals were mostly observed at night while sleeping on low thin branches or during the day while actively moving around on larger trunks of mopane trees.

***Lygodactylus nyaneka* Marques, Ceríaco, Buehler, Bandeira, Janota & Bauer, 2020**
Figure 5H

Material examined. ANGOLA – **Namibe Province** • Humbi; −16.9853, 012.5419; 890 m a.s.l.; FKH 0813–0815; GenBank: ON006617–ON006619 • Lutuima–Muinde road; −16.8363, 012.6983; 845 m a.s.l.; FKH 0613–4; GenBank: ON006620 • Quedas do Montenegro; −16.9968, 013.2480; 627 m a.s.l.; FKH 0678; GenBank: ON006621 • Mupaka camp; −16.8433, 012.6888; 847 m a.s.l.; FKH 0682; GenBank: ON006622 • Espinheira; −16.7855, 012.3589; 454 m a.s.l.; FKH 0332.

Identification. A small gecko (SVL 26–34 mm) that can be distinguished from its Angolan congeners by fewer cloacal pores than *L. angolensis* and more than *L. lawrencei* and *L. tchokwe*, and the lack of gular coloration present in *L. chobiensis* and *L. baptistai* (Marques et al. 2020). There is low intraspecific divergence for 16S (Table S2) but much larger genetic distance (~12.5%) to the most closely related species (*L. lawrencei*) ocurring in sympatry in Iona NP.

Biology and distribution. *Lygodactylus nyaneka* is the most widespread species of Angolan *Lygodactylus*, occurring from 500–2000 m a.s.l. (Marques et al. 2020). This species is apparently common in Huila and northern Namibe provinces. However, only one record had been documented from southern Namibe Province, from between Ouipaca and Otchifengo on the eastern edge of Iona NP (Marques et al. 2020). Here, we report on additional specimens collected at Espinheira and ~30 km southeast of Espinheira, and at Humbi (Fig. 2N), where it was found in syntopy with *L. lawrencei*. Additional specimens were collected at Tchitchaki River (Fig. 2F) on the edge of the sand desert; between Lutuima and Muinde; near Mupaka, in arid savanna; at Montenegro, corresponding to the southernmost record in the park. These records suggest this species to be the most common species in the genus *Lygodactylus* within Iona NP, while extending its known distribution in the country. Individuals were found at night while sleeping on thin lower vertical branches or during day moving among the trunks of trees.

***Pachydactylus caraculicus* FitzSimons, 1959**
Figure 5I

Material examined. ANGOLA – **Namibe Province** • Mongo; −17.0398, 012.6010; 917 m a.s.l.; JLRZC0137,

FKH 0803–7; GenBank: ON006623–ON006627 • Manaculama; −16.8193, 012.7188; 793 m a.s.l.; FKH 0808; GenBank: ON006628.

Identification. This species is a small-bodied *Pachydactylus* (SVL 30–40 mm), characterized by its lateral yellow and black bands across the entire dorsum, more marked in juveniles. The 16S sequences demonstrate that the new material does not differ substantially from material collected at Epupa Falls in Namibia (~0.5%; GenBank accession: AY123377; Table S2).

Biology and distribution. It was described from Caraculo, Namibe Province, Angola and is widely distributed from northwestern Namibia to southern Benguela Province (Marques et al. 2018). This gecko is commonly found in crevices of small granitic boulders (usually <1 m in size; Fig. 2N). Our new records represent the first from within Iona NP and the southernmost for Angola, closing a major geographic gap between Angolan and Namibian records. Specimens were found at night in a transition zone of large granitic rocks and conglomerates at the edge of a mountain range. Interestingly, all the specimens were found in March and most of them were juveniles or semi-adults, with just one adult collected.

***Pachydactylus* cf. *oreophilus* McLachlan & Spence, 1967 complex**

Figure 5J

Material examined. ANGOLA – **Namibe Province** • Omauha; −16.1983, 012.4111; 356 m a.s.l.; FKH 0340, FKH 0349, 0350, P9.281– P9.283; GenBank: ON006629–ON006634 • Tchamalindi; −16.9721, 012.8862; 1364 m a.s.l.; P1.105; GenBank: ON006635 • Cunene River to Tchinhungua 2; −17.2627, 012.4460; 250 m a.s.l.; P1.83–5; GenBank: ON006636, ON006637.

Identification. *Pachydactylus oreophilus* is a rock-dwelling species (SVL 40–50 mm), that was originally described from Sesfontein, Namibia (McLachlan and Spence 1967). An unpublished phylogenetic analysis suggests that the Angolan material represents more than one undescribed species from a monophyletic group within the *P. oreophilus* complex (A. Bauer unpubl. data 2021). Individuals from Iona NP lowlands differed from highland populations by 11.2%, suggesting there is species level differentiation between them, warranting further investigation (Table S2).

Biology and distribution. Individuals were commonly found actively hunting insects at night while moving on large boulders and cliffs and sometimes jumping to the ground running between rocks. These geckos were also found during the day hiding in rock crevices, both in lowlands and highlands. They were often found in syntopy with *Rhoptropus boultoni* and *R. biporosus*, even using the same rocks.

***Pachydactylus parascutatus* Bauer, Lamb & Branch, 2002**

Figure 5K

Material examined. ANGOLA – **Namibe Province** • Tchinhungua; −17.2257, 012.4369; 249 m a.s.l.; FKH 0605, FKH 0606; GenBank: ON006638, ON006639 • Garota Nova; −17.1526, 012.7476; 370 m a.s.l.; FKH 0684–06846, P1.276; GenBank: ON006640–ON006642 • Cunene River to Tchinhungua 2; −17.2628, 012.4461; 250 m a.s.l.; FKH 0566–7, P1.85, P1.87 & P1.89–90; GenBank: ON006644–ON006647.

Identification. A medium-sized *Pachydactylus* (SVL 35–38.5 mm), that can be differentiated from *P. scutatus*, the most morphologically similar species in Iona NP, by the lack of a bright nuchal band around the neck and more slender body. DNA barcoding shows that these specimens are divergent by ~3% (16S) from those recorded at topotypic locality in Sesfontein, Namibia (GenBank accession: AY123383).

Biology and distribution. This species was previously only known from Opuwo District, Namibia, recorded from arid areas of the Namibian Kaokoveld where it utilised shrubs and grasses as substrate (Bauer et al. 2002). Here we report on new specimens recorded from the southern parts of Iona NP, along the margins of the Cunene River, at Garota Nova and around Tchinhungua. The individuals were always found at night and in close association with thick bushes of toothbrush trees, *Salvadora persica*, proving to be very difficult to catch. Sometimes, specimens were observed foraging among thin branches of *Salvadora* bushes but would readily drop to the ground when disturbed and disappear underneath the bush among leaf litter. Most often, they were observed cautiously walking on the ground among the thick layer of dry *Salvadora* leaves, at the edge but never venturing outside the protection of the main bush. These records extend the known species distribution some ~230 km north, being the northernmost for the species and the first records in Angola

***Pachydactylus* cf. *punctatus* Peters, 1854 complex**

Figure 5L

Material examined. ANGOLA – **Namibe Province** • Omauha; −16.1983, 012.4111; 356 m a.s.l.; FKH 0793, FKH 0801; GenBank: ON006648, ON006649 • Uaua; −16.8454, 012.6135; 819 m a.s.l.; JLRZC0140; GenBank: ON006650 • Mondelalola; −16.8690, 012.5870; 773 m a.s.l.; JLRZC0141, JLRZC0142; GenBank: ON006651, ON006652 • Mupaka camp; −16.8434, 012.6889; 847 m a.s.l.; FKH 0680; GenBank: ON006653 • Espinheira; −16.7856, 012.3589; 454 m a.s.l.; PEM R17942– R17945, JLRZC0131– JLRZC0133, P1.270, P1.277, FKH 0333, FKH 0802; GenBank: ON006654–ON006658 • Tchamalindi; −16.9751, 012.8857; 1434 m a.s.l.; FKH 0572, 0573, P1.109; GenBank: ON006659–ON006661 • Serra Cafema; −17.1270, 012.5126; 2033 m a.s.l.; P1.125; GenBank: ON006662 • Vitambi; −17.0822, 012.2637; 549

m a.s.l.; FKH 0601; GenBank: ON006663 • Tchinhungua; −17.2258, 012.4369; 249 m a.s.l.; FKH 0607–8; GenBank: ON006664, ON006665 • Lutuima–Muinde road; −16.8363, 012.6983; 845 m a.s.l.; FKH 0612 • Otchifengo River; −16.6391, 012.9272; 605 m a.s.l.; FKH 0670–2; GenBank: ON006666–ON006668 • Mupaka camp; −16.8434, 012.6889; 847 m a.s.l.; FKH 0681; GenBank: ON006669 • Muende River; −16.5213, 012.3140; 316 m a.s.l.; P1.82; GenBank: ON006670.

Identification. *Pachydactylus punctatus* is a small *Pachydactylus* (SVL 25–35 mm), described from central Mozambique (Peters 1854). However, the taxonomic status of this species has remained controversial due to large geographic overlap with closely related species, and there is high genetic divergence within *Pachydactylus punctatus* sensu lato, with at least four different putative species occurring in Angola (H. M. Heinz unpubl. data 2018). The material collected during our surveys show the presence of two sister clades that differ from each other by ~8% (16S).

Biology and distribution. This species is a small, ground-dwelling *Pachydactylus*. However, due to the large number of cryptic species of *Pachydactylus*, the biology and distribution remains unresolved. The two sister clades reported here appear to be ecologically segregated, with one occurring on sandy substrate of the central plains and the other associated with mountain ranges foraging on rocky ground near rocky outcrops.

Pachydactylus rangei Andersson, 1908

Figure 5M

Material examined. ANGOLA – **Namibe Province** • Foz do Cunene; −17.2600, 011.7900; TM 40663, TM 40707; historical material • Lacrau, 12 km NW of Foz do Cunene; –17.2000, 011.8300; TM 40700–3; historical material • Cunene River Baptista camp; –17.1605, 012.0172; 104 m a.s.l.; FKH 0327, 0330, 0331; GenBank: ON006671–ON006673.

Identification. *Pachydactylus rangei* (SVL 60–65 mm) can be distinguished from other *Pachydactylus* by presence of webbed membranes between digits of the manus and pes. DNA barcoding revealed low divergence among Angolan specimens (Table S2) but differing by ~2.5% from material collected ~800 km south from Rooibank, Namibia (GenBank accession: AY123375).

Biology and distribution. This species is the only gecko adapted to live in the soft sand dunes of the Namibe Desert (Bauer and Lamb 2005) and occurs in the dune sand seas of Iona NP. It was often observed at night foraging on the sand and sometimes moving marginally out of dunes onto the sandy areas of Tchitchaki and Curoca riverbeds which delimit the dunes in the east and north, respectively.

Pachydactylus cf. *rugosus* Smith 1849

Figure 5N

Material examined. ANGOLA – **Namibe Province** • Lutuima–Muinde road; −16.8363, 012.6983; 845 m a.s.l.; FKH 0611; GenBank: ON006674.

Identification. A medium-sized gecko (SVL 45–60 mm), morphologically well differentiated from other members of the genus *Pachydactylus* by the presence of strongly mucronate head and body and a dorsal colour pattern consisting of a series of five light brown blotches between the nape and the sacrum (Lamb and Bauer 2000). However, a phylogenetic analysis shows two different clades within *P. rugosus*, which differ by >15% uncorrected net *p*-distances for ND2 (W. Conradie unpubl. data 2021). The specimens for which we produced 16S sequences are most similar to the northern Namibian material and might represent an undescribed taxon.

Biology and distribution. *Pachydactylus rugosus* is a small-bodied generalist species of the genus *Pachydactylus* (Heinicke et al. 2011), widely distributed from the Northern Cape Province, South Africa, to the northwestern region of Namibia (Lamb and Bauer 2000). The species had not been recorded in Angola until very recently (Branch et al. 2019c; Bates et al. 2020). Nevertheless, two new photographic records from coastal areas in Namibe Province have been added to the known distribution of the species (W. Conradie unpubl. data 2021). We collected one specimen on 8 August 2021 between Lutuima and Muinde in Iona NP. This represents the second specimen collected for Angola and the first in Iona NP.

Pachydactylus scutatus Hewitt, 1926

Figure 5O

Material examined. ANGOLA – **Namibe Province** • Curoca River at Omauha Water Cistern; −16.2648, 012.3224; 185 m a.s.l.; FKH 0784 & FKH 0786; GenBank: ON006675 – ON006676 • Otchifengo River; −16.6391, 012.9271; 605 m a.s.l.; FKH 0668; GenBank: ON006677 • Quedas do Montenegro; −16.9969, 013.2480; 627 m a.s.l.; FKH 0676–7 GenBank: ON006678 – ON006679 • Espinheira; −16.7856, 012.3589; 454 m a.s.l.; P1.271.

Identification. *Pachydactylus scutatus* is a medium-sized *Pachydactylus* (SVL 30–40 mm), sister to *P. angolensis* (Bauer and Branch 2002). It can be distinguished by the presence of a white nuchal collar. One juvenile (JLRZC0111) had a bright yellow body and a white collar and was found under a rock. Our specimens differ ~7.6% from material of *P. scutatus* collected close to the type locality (Kowaris, Kaokoveld, Namibia) of the species (GenBank accession: AY123381; Table S2), warranting further investigation.

Biology and distribution. This species has been reported to be very rare in Angola and the few known records for the country originated from Iona NP (Ceriaco et al. 2016; Branch et al. 2017). During our surveys, some individuals were found at night moving rapidly between boulders on the edge of the sand dunes (Fig. 2C), while others were found sheltering under exposed tree roots along the banks of a dry riverbed. Surprisingly, one individual was observed diving under the soft sand to hide.

We cannot confirm whether this observation is typical behaviour of the species.

***Pachydactylus vanzyli* (Steyn & Haacke, 1966)**
Figure 5P

Material examined. ANGOLA – **Namibe Province** • Cacolo Windmill, 20 km W of Iona; −16.8568, 012.4334; 572 m a.s.l.; TM 40711–40717; historical material • Espinheira; −16.7856, 012.3589; 454 m a.s.l.; FKH 0598– 0600, FKH 0334–0337; GenBank: ON006680–ON006685 • Vitambi; −17.0822, 012.2637; 549 m a.s.l.; FKH 0602–4; GenBank: ON006686–ON006688 • Muende River; −16.5212, 012.3140; 314 m a.s.l.; P1.78; GenBank: ON006689.

Identification. *Pachydactylus vanzyli* is a medium-sized to large (SVL 50–55 mm) nocturnal gecko from the Namib Desert that differs from *P. rangei*, its closest related species, by reduced webbing in the foretoes. The individuals sequenced show low divergence between them (1.66%; Table S2) but high sequence divergence (~9%) with material collected from Orupenbe and Ondonduiengo, Namibia (GenBank accession: DQ278600). This latter comparison suggests unrecognised species level divergence, and a detailed morphological and phylogenetic analysis of this group is needed.

Biology and distribution. It was described from northwestern Namibia and only a few records are known from Angola (Marques et al. 2018). During our expeditions, we recorded several specimens from different locations, observed at night on flat gravel and sandy plains across Iona NP. Individuals were observed emerging at dusk from holes in the sand, with others finding refuge under welwitschias, or actively hunting termites and other insects. One specimen was regurgitated by a *Bitis caudalis*, which is commonly found in the same habitat as *P. vanzyli*. We observed clear habitat segregation with its sister species *P. rangei,* which were only recorded in softer sandy dunes of the desert. Here we report for the first time a neon green fluorescence in the species (Fig. 6), which has only been observed previously in *P. rangei* (Prötzel et al. 2021), suggesting some iridophore adaptation within this group.

***Rhoptropus afer* Peters, 1869**

Material examined. ANGOLA – **Namibe Province** • Foz do Cunene; −17.2600, 011.7900; TM 40655–7, TM40672–4; historical material • Lacrau 12km NW from Foz do Cunene; −17.2000, 11.8300; TM 40699; historical material.

Identification. *Rhoptropus afer* is the most distinctive species in the genus. A small species (SVL 35–53 mm) with relatively short, stout toes, with 5 or 6 small subdigital pads, and considerably elongate hind limbs in comparison to the front limbs (Kuhn 2016). There are no preanal pores. The back is light olive to grey-brown, with scattered red-brown and light cream spots.

Biology and distribution. *Rhoptropus afer* occurs in northern Namibia and southern Angola (Marques et al. 2018) and is associated with large flat boulders (Kuhn 2016). Only a few scattered records have been published

Figure 6. *Pachydactylus vanzyli* in lateral view under (**A**) natural light, and (**B**) 467 nm UV light, showing the green fluorescence around the eyes, and on flanks. Photos by JLR.

for Angola and their identification is questionable due to lack of a full assessment of morphological traits and no corresponding genetic data to corroborate their identification. Most of the records in the literature date from the 19th century, where the species was reported from Curoca River, Moçamedes, Maconjo, Capangombe and even as far north as Hanha, in Benguela Province (Bocage 1895; Marques et al. 2018). Here, we report on previously unpublished material from Foz do Cunene, where several specimens were collected in 1971 but whose identification has not been confirmed by genetic data. Reportedly, the specimens were found during the day on small boulders (<1 m in size) that break the sand surface of the dunes near Foz do Cunene. Recent attempts to collect additional material of this species from Foz do Cunene were unsuccessful. All recent material collected from that area have been identified as *Rhoptropus biporosus* by DNA (e.g., GenBank accession: AY026928).

***Rhoptropus barnardi* Hewitt, 1926**
Figure 5Q

Material examined. ANGOLA – **Namibe Province** • Tonombe; −17.0964, 012.3035; 615 m a.s.l.; JLRZC0122, JLRZC0126, JLRZC0127; GenBank: ON006690–ON 006692 • 40 km S of Omauha Lodge; −16.5117, 012.4476; 369 m a.s.l.; PEM R19981 • Iona Mountain; −16.9103, 012.5888; 1243 m a.s.l.; PEM R19982 • Espinheira; −16.7886, 012.3584; 456 m a.s.l.; PEM R19983 • Road from Espinheira to Iona; −16.8349, 012.4469; 592 m a.s.l.; PEM R19984 • Tchamalindi; −16.9756, 012.8856; 1436 m a.s.l.; FKH 0575, P1.101; GenBank: ON006693, ON006694 • Serra Cafema; −17.1269, 012.5126; 2033 m a.s.l.; P1.120, P1.122, P1.124; GenBank: ON006695, ON006696 • Quedas do Montenegro; −16.9969, 013.2480; 627 m a.s.l.; FKH 0679; GenBank: ON006697 • Cunene River to Tchinhungua 2; −17.2626, 12.4461; 250 m a.s.l.; FKH 0568, P1.88; GenBank: ON006698 • 26 km E of Iona; −16.7006, 012.8242; 625 m a.s.l.; PEM R19985, R19986.

Identification. This species is a medium-sized (SVL 40–46 mm), rock-dwelling diurnal gecko. Males have 4–7 preanal pores arranged in a single row. The middle row of scales under the tail is not enlarged. The scales on the back are slightly keeled and tubercular (Kuhn 2016). DNA sequences of specimens from Iona NP showed little within-species divergence (Table S2) but differ by a ~6% difference from specimens collected from Ugab River mouth, Namibia (GenBank accession: AY026929).

Biology and distribution. This species is commonly found on smaller boulders or rock piles (Kuhn 2016). Originally described from Cunene Province, Angola, *Rhoptropus barnardi* is often observed in northwestern Namibia. Only a few records of this species had been reported from the northern edge of Iona NP and surrounds (Ceríaco et al. 2016a). However, morphological similarities to an undescribed species of the genus *Rhoptropus* could have led to misidentification (Kuhn 2016). Our DNA sequences allow us to confirm the presence of *Rhoptropus barnardi* within Iona NP, and it is widely distributed across the park, from sea level near the Cunene River to the highlands in Tchamalindi and Cafema Mountains.

***Rhoptropus biporosus* FitzSimons, 1957**
Figure 5R

Material examined. ANGOLA – **Namibe Province** • 10 km south of Red Canyon camp; −15.8306, 012.1412; 110 m a.s.l.; PEM R19951 • 28 km NE from Foz do Cunene; −17.1083, 012.0036; 422 m a.s.l.; PEM R19952, R19953 • Road to Tambor; −15.8761, 012.2058; 190 m a.s.l.; PEM R19944– R19949 • Carinhambi; −17.0989, 011.9187; 352 m a.s.l.; FKH 0683 • Espinheira; −16.7856, 012.3589; 454 m a.s.l.; JLRZC0128, PEM R19957, TM 40611–40614, TM 40630–40639; GenBank: ON006699 • Foz do Cunene; −17.2638, 011.7950; 10 m a.s.l.; TM 40675–84, TM 40694, TM 40645–40654, P1-167, FKH 0596, 0597; GenBank: ON006700–ON006702 • Guelengue; −16.9591, 012.0359; 469 m a.s.l.; JLRZC0118; GenBank: ON006703 • 40 km S of Omauha Lodge; −16.5116, 012.4476; 369 m a.s.l.; PEM R19955, R19956 • Road to Omauha Lodge; −15.8843, 012.2818; 229 m a.s.l.; PEM R19950.

Identification. This is a small (SVL 40–45 mm) diurnal species in which males are characterized by having two precloacal pores (Kuhn 2016). Our 16S sequences revealed low intraspecific divergence (Table S2).

Biology and distribution. In Angola, it is only known to occur in southern Namibe Province (Marques et al. 2018), being commonly observed in the central and southern regions of Iona NP (Ceríaco et al. 2016a). Specimens reported here were observed during the day actively moving around granitic boulders or between small rocks and vegetation on the central plains.

***Rhoptropus boultoni* Schmidt, 1933**
Figure 5S

Material examined. ANGOLA – **Namibe Province** • 10 km S of Red Canyon camp; −15.8305, 012.1412; 110 m a.s.l.; PEM R19961, R19962, R19987 • Road to Omauha Lodge; −15.8842, 012.2818; 229 m a.s.l.; PEM R19963, R19964 • Omauha Lodge; −16.5117, 012.4476; 369 m a.s.l.; PEM R19966, P9.277, FKH 0347, 0348; GenBank: ON006708–ON006710 • Iona Mountain; −16.9103, 012.5888; 1243 m a.s.l.; PEM R19967 • 8 km NE from Iona; −16.8475, 012.6155; 796 m a.s.l.; PEM R19968, R19969 • Serra Cafema; −17.1269, 012.5126; 2033 m a.s.l.; P1.123; GenBank: ON006704 • Cunene River Baptista camp; −17.1606, 012.0172; 74 m a.s.l.; P9.252–3; GenBank: ON006705, ON006706 • 5 km NE of Cunene camp; −17.1275, 012.0094; 390 m a.s.l.; P9.262; GenBank: ON006707.

Identification. This species is the largest Angolan *Rhoptropus* (SVL 55–74 mm), characterized by its orange-spotted dorsum. DNA barcoding shows high genetic

differentiation (>4.5% divergence) within Iona NP (Table S2), and also compared with material collected near the Skeleton Coast National Park, Namibia (GenBank accession: AY026930).

Biology and distribution. This large rupicolous species is likely the most commonly observed species in the genus *Rhoptropus* in Angola, widely distributed in the southwestern regions. In Iona NP, this gecko has been recorded from most habitats except the dunes (Ceríaco et al. 2016a). The species has been reported from sea level to 2000 m a.s.l., associated with large boulders where they actively hunt both during day and night. It is frequently found in syntopy with other *Rhoptropus* congeners.

***Rhoptropus* sp.**
Figure 5T

Material examined. ANGOLA – **Namibe Province** • Salondjamba; −16.3070, 012.4195; 204 m a.s.l.; FKH 0819, 0820, FKH 0829; GenBank: ON006711, ON006712.

Identification. This is a potentially undescribed endemic Angolan species which is morphologically similar to *R. barnadi* but genetically closer to *R. biporosus* (Kuhn 2016; A. Bauer and A. Kuhn unpubl. data 2021). This species has been previously reported from Iona NP by Ceríaco et al. (2016a).

Biology and distribution. Even though the biology and real distribution remains unclear, this species has been found on granitic boulders during the day and rarely at night. It has been found in syntopy with related species, such as *R. boultoni.* The specimens were collected at Salondjamba, near the Curoca River at the main entrance to Iona NP, and we attribute them to this undescribed species because they cannot be morphologically or genetically ascribed to any other known species.

Cordylidae

***Cordylus namakuiyus* Stanley, Ceríaco, Bandeira, Valerio, Bates & Branch, 2016**
Figure 7A

Material examined. ANGOLA – **Namibe Province** • Serra Cafema; −17.1269, 012.5126; 2033 m a.s.l.; FKH 0576, FKH 0578, FKH 0581, Pl.129, Pl.130; GenBank: ON006713–ON006718.

Identification. This species is the only girdled lizard (SVL 81.83–101.09 mm) known from the coastal plain of Angola. DNA barcoding revealed little differentiation between the newly collected material (Table S2) and the paratype material from approximately 50 km north of Iona NP (Stanley et al. 2016).

Biology and distribution. *Cordylus namakuiyus* is a rupicolous species endemic to coastal southwestern Angola (Stanley et al. 2016). The southernmost record for the species was previously reported from 20 km north of the Iona NP entrance of Salondjamba. Herein we report the species from the mountain peak of Serra Cafema within Iona NP, extending the known distribution 150 km southwards and increasing its elevation range to over 2000 m a.s.l. These new records breach the distribution gap between Angolan and Namibian material and may suggest that historical material from Baynes and Otjihipa mountians in northern Namibia belongs to this species, instead of *C. machadoi* as previously suggested by Stanley et al. (2016). Recently DeBoer et al. (2019) presented morphological results that further support this notion but caution that molecular data is needed to truly resolve the taxonomic status of Namibian material. Newly collected genetic material from Otjihipa Mountains may help resolve this issue (F. Becker et al. unpub. data. 2021).

Gerrhosauridae

***Cordylosaurus subtessellatus* (Smith, 1844)**
Figure 7B

Material examined. ANGOLA – **Namibe Province** • Espinheira; −16.7454, 012.3687; 437 m a.s.l.; photographic record.

Identification. *Cordylosaurus* is a monotypic genus of plated lizard, characterized by its small size (SVL 35–45 mm), black middorsal stripe from head to tail, and its bright blue tail (Branch 1998).

Biology and distribution. This species is diurnal, moving rapidly between small stones in the gravel plains and will quickly shed its tail when disturbed (Branch 1998). Despite no voucher specimens being collected during our surveys, a specimen was photographed on the gravel plains northeast of Espinheira. It has been reported from various localities in Namibe Province including Iona NP (Ceríaco et al. 2016a; Marques et al. 2018), with a few additional ad hoc sightings in the park from sea level to 500 m a.s.l., and also above 1400 m a.s.l. on Mount Tchamalindi.

***Gerrhosaurus skoogi* Andersson, 1916**
Figure 7C

Material examined. ANGOLA – **Namibe Province** • Curoca River at Omauha Water Cistern; −16.2647, 012.3223; 185 m a.s.l.; JLRZC0112; GenBank: ON006719 • Tchitchaki Valley; −16.2850, 012.2815; 219 m a.s.l.; JLRZC0116; GenBank: ON006720.

Identification. *Gerrhosaurus skoogi* is a large lizard (SVL 110–150 mm) adapted to live on sand dunes, identified by its large size and its modified rostral scales (Branch 1998). Specimens collected from Curoca River at the northern edge of the dune desert and Tchitchaki differed genetically by 2.2% for 16S (Table S2) and approximately 6% when compared with material from Ondonduiengo River, Namibia (GenBank accession: AY167364).

Biology and distribution. This species occurs from northwestern Namibia to southwestern Angola (Branch 1998). Individuals are usually found in groups close to the summit of large dunes where there is sufficient vegetation for them to shelter or where the loose sand allows for easy sand-diving. The tracks of this species are easily

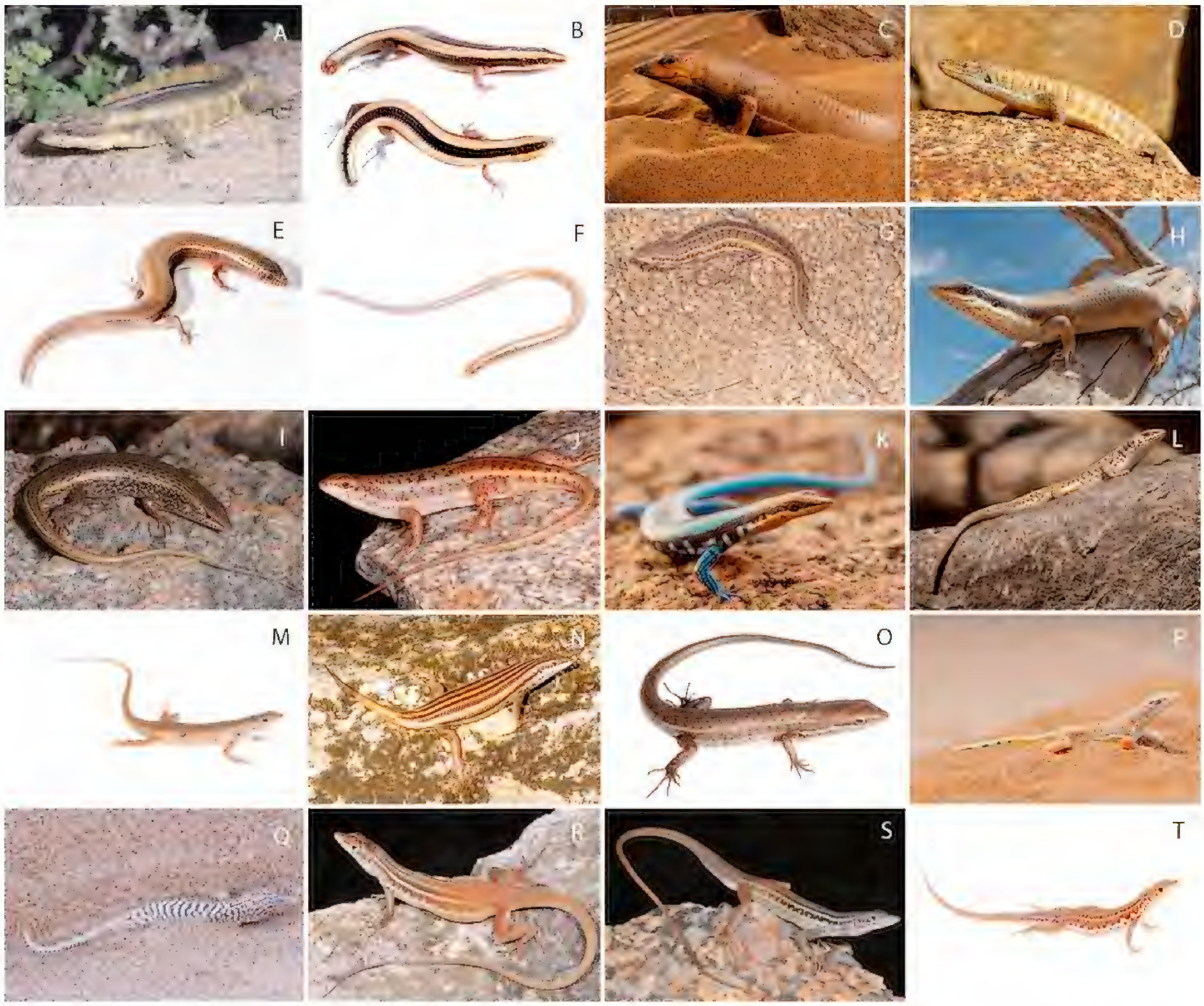

Figure 7. Species in the families Lacertidae. Gerrhosauridae and Scincidae from Iona National Park. **A.** *Cordylus namakuiyus*. **B.** *Cordylosaurus subtessellatus*. **C.** *Gerrhosaurus skoogi*. **D.** *Matobosaurus maltzahni*. **E.** *Panaspis mocamedensis*. **F.** *Typhlacontias punctatissimus bogerti* **G.** *Trachylepis acutilabris*. **H.** *Trachylepis binotata*. **I.** *Trachylepis* cf. *chimbana*. **J.** *Trachylepis hoeschi*. **K.** *Trachylepis laevis*. **L.** *Trachylepis occidentalis*. **M.** *Trachylepis punctulata*. **N.** *Trachylepis sulcata*. **O.** *Trachylepis* sp. **P.** *Meroles anchietae*. **Q.** *Meroles reticulatus*. **R.** *Pedioplanis haackei*. **S.** *Pedioplanis huntleyi*. **T.** *Pedioplanis serodioi*. Photographs by JLR (B, C, F, H, K–P. T). William R. Branch (D, J, R, S) and PVP (A, E,. G, I, N, O, Q).

recognizable in the loose dune sands, given their large size and characteristic pattern. Specimens and tracks of *G. skoogi* were observed in most dune areas surveyed, absent only in the central mobile dunes. Lizards were spotted during the day and at dusk.

***Matobosaurus maltzahni* (de Grys, 1938)**
Figure 7D

Material examined. ANGOLA – **Namibe Province** • Omauha Lodge; −16.2006, 012.4018; 341 m a.s.l.; PEM R17984–5 • Pediva camp; −16.2173, 012.5167; 329 m a.s.l.; photographic record.

Identification. This is a large (SVL 285 mm), rock-dwelling plated lizard, indentified by its large size and plated-like scales.

Biology and distribution. *Matobosaurus maltzahni* is commonly observed basking on the tops of big boulders or hiding on the ground between closely spaced large boulders (Bates et al. 2013). The species is widely distributed in the rocky and mountainous areas of Iona NP and across southwestern Angola (Marques et al. 2018).

Agamidae

***Agama anchietae* Bocage, 1896**
Figure 4F

Material examined. ANGOLA – **Namibe Province** • 26 km W from Oncócua; −16.7500, 013.2300; TM 40768, TM 40772; historical material • 45 km S of Omauha Lodge; −16.5369, 012.4410; 375 m a.s.l.; PEM R19920 • 5 km N of Espinheira; −16.7450, 012.3817; 440 m a.s.l.; PEM R19924 • 8 km NE of Iona; −16.8291, 012.6211; 740 m a.s.l.; PEM R19925–R19928 • Tchamalindi; −16.9754, 012.8858; 1434 m a.s.l.; P1.94, P1.107; GenBank: ON006721.

Identification. *Agama anchietae* is a small terrestrial lizard (SVL 60–80 mm), with a broad head and a short, rounded snout. Body short with strongly keeled dorsal scales and pale brown coloration, except for reproductive males who display varied color on the dorsum (Branch

1998). DNA sequences showed little divergence (<1%) among newly collected specimens and material from adjacent Namibia (GenBank accession: GU128446)

Biology and distribution. This species is widely distributed in the semi-desert and arid savanna of South Africa, Namibia, and southern Angola (Branch 1998). It is commonly found in Iona NP (Ceríaco et al. 2016a), except in the western dune fields. Individuals are often observed basking on top of small rocks or low branches and quickly seek cover under rocks or in holes when disturbed. We found that the species occurs in both the lowlands and highlands up to 2000 m a.s.l.

***Agama planiceps* Peters, 1862**
Figure 4G

Material examined. ANGOLA – **Namibe** Province • Foz do Cunene; −17.2600, 011.7900; TM 40665–40668, TM 40695; historical material • Omauha Lodge; −16.2006, 012.4018; 341 m a.s.l.; photographic record • Serra Cafema; −17.1269, 012.5126; 2033 m a.s.l.; photographic record.

Identification. This species can be differentiated from *A. anchietae* based on the large body (SVL 80–100 mm) and distinctive coloration (red-blue in males, characteristic yellow head in females). The Angolan *Agama planiceps* complex comprises multiple, distinct genetic lineages (Butler 2019). The material from the arid Iona NP matches that of the "typical" *A. planiceps.*

Biology and distribution. This is a rock-dwelling agamid that appears to be abundant in arid regions of Namibia and southwestern Angola (Branch 1998). The species is often observed within Iona NP (Ceríaco et al. 2016a) and throughout Namibe and Benguela provinces (Marques et al. 2018). Individuals were only recorded during the day, mainly associated with large granitic boulders, where they bask on top of the rocks. They seek shelter in deep rock crevices. They were also observed at times climbing trees or running on the ground between boulders.

Scincidae

***Panaspis mocamedensis* Ceríaco, Heinicke, Parker, Marques & Bauer, 2020**
Figure 7E

Material examined. ANGOLA – **Namibe Province** • Tchamalindi; −16.9757, 012.8856; 1434 m a.s.l.; P1.114; GenBank: ON006722.

Identification. *Panaspis mocamedensis* is a small lizard (SVL 26.5–32.5 mm). This species may be distinguished from congeners by the absence of supranasal, fused frontoparietal, and ablepharine eye (Ceríaco et al. 2020c). Our collected specimen is genetically similar to the type material of *Panaspis mocamedensis* (~0.2%) from Virei, Namibe, Angola (GenBank accessions: MN846701, MN846702).

Biology and distribution. This species was described from Virei and Maungo, Namibe Province and was only known previously from the type series (Ceríaco et al. 2020c). Our collected specimen from Tchamalindi Mountain provides a range extension of ~150 km southwards and represents the first record for Iona NP. This record also increases the known elevational range from 523 m a.s.l to more than 1400 m a.s.l. Several individuals were observed during the day, moving quickly among leaf litter in mopane savanna on the rocky slopes of Tchamalindi.

***Typhlacontias johnsonii* Andersson, 1916**

Material examined. ANGOLA – **Namibe Province** • Lacrau; −17.2000, 011.8300; TM 40704–40706; historical material.

Identification. This species is a small (SVL 80–100 mm) and slender skink. Specimens of *T. johnsonii* have not been collected in recent years and the species is only known from the type specimens from Tômbwa (Andersson 1916) and material collected in the 1970s (Haacke 1997). On the loose sand at the base of very shallow dunes, we observed sinuous subterranean tracks that we tentatively ascribed to this species. However, no individuals were observed. Because earlier records of this species were all from sandy habitat, and no other small subterranean serpentiform species is known to occur in that habitat, we believe that they may be *T. johnsonii.*

***Typhlacontias punctatissimus bogerti* (Laurent, 1964)**
Figure 7F

Material examined. ANGOLA – **Namibe Province** • Espinheira; −16.7886, 012.3584; 456 m a.s.l.; PEM R18045, R18046 • Tchitchaki Valley; −16.2891, 012.3180; 248 m a.s.l.; FKH 0787; GenBank: ON006723 • 43 km 250° from Espinheira; −16.9186, 011.9756; 371 m a.s.l.; FKH 0797; GenBank: ON006724 • Road to Foz do Cunene 40 km SW of Espinheira; −16.9577, 012.1238; 537 m a.s.l.; FKH 0798; GenBank: ON006725.

Identification. *Typhlacontias* was last reviewed by Haacke (1997) who validated the status of *Typhlacontias punctatissimus bogerti* based on morphological evidence. The material here reported exhibit the diagnostic character of the *T. p. bogerti* (second and third upper labial reaching eye, and small body size (SVL 60–80 mm)). However, DNA barcoding shows high sequence divergence (>7%) between specimens collected at Skeleton Coast Park, Namibia (GenBank ascension: DQ316889) and those collected at Iona NP, although variation within the latter was low (Table S2).

Biology and distribution. This species was previously recorded from Espinheira (Ceríaco et al. 2016a) and is commonly found in the central plains of Iona NP, under dead welwitschias, fallen logs, dead wood, and accumulations of leaves in riverine areas.

***Trachylepis acutilabris* (Peters, 1862)**
Figure 7G

Material examined. ANGOLA – **Namibe Province** •

Espinheira; −16.7856, 012.3589; 454 m a.s.l.; TM 40628, TM 40629, PEM R18019, PEM R18022, PEM R18035, PEM R18036 • Otchifengo River; −16.6900, 013.0100; TM 40774; historical material • Iona 6 km S of Rio Curoca; −16.3400, 012.4400; TM 40581–9; historical material.

Identification. A small terrestrial skink (SVL 40–55 mm) that was identified based on its characteristic colour pattern, by having three keels on each dorsal scale, 28–32 rows of scales around midbody, and the characteristic upper lip (Branch 1998).

Biology and distribution. This species is frequently found in sandy areas of Namibia and Angola (Branch 1998; Marques et al. 2018). This is one of the most frequently observed species in the genus *Trachylepis* in southern Namibe Province, including Iona NP (Ceriaco et al. 2016a). Individuals were observed in all regions of the park, showing a remarkable color variation that matched the substrate where they occurred, ranging from white to bright orange/red. The species is most commonly encountered in open areas, moving between small rocks, succulent plants, and small bushes.

***Trachylepis binotata* (Bocage, 1867)**
Figure 7H

Material examined. ANGOLA – **Namibe Province** • Iona Nature Reserve (without precise locality); TM40765; historical material • 12 km from Oncócua; −16.7100, 013.3200; TM 40738, TM 40770; historical material • Otchifengo River; −16.6391, 012.9272; 605 m a.s.l.; photographic record.

Identification. This species is identifiable by its large size (SVL 80–120 mm), dorsal scales with three keels, and characteristic black spots with light flecks on each side of the head (Branch 1998).

Biology and distribution. *Trachylepis binotata* is a large arboreal skink commonly found in mopane trees along dry riverine areas (Branch 1998). Several individuals were observed on riverine trees along drainage lines in the southern and eastern regions of Iona NP, usually moving or basking on Mopane or *Senegalia* trees. During the March 2021 survey, several specimens were observed and photographed.

***Trachylepis* cf. *chimbana* (Boulenger, 1887)**
Figure 7I

Material examined. ANGOLA – **Namibe Province** • Serra Cafema; −17.1269, 012.5126; 2033 m a.s.l.; P1-118; GenBank: ON006726 • Tchamalindi; −16.9767, 012.8783; 1523 m a.s.l.; FKH 0570.

Identification. A slender, ground-dwelling species in the *T. lacertiformis* group, distributed from southwestern Angolan and northwestern Namibia (Broadley 1975). The original description by Boulenger (1887) is not detailed or comprehensive, and the lack of recent topotypic material has led to the taxonomic status of this species becoming unclear and in need of revision (Marques et al. 2018). The DNA sequences from the specimens collected during our surveys show very low divergence (0.6%) from those previously collected 16 km west of the bottom of Leba Pass (GenBank accession: MK792061) which were assigned to this species based on morphology (Weinell et al. 2019).

***Trachylepis hoeschi* (Mertens, 1954)**
Figure 7J

Material examined. ANGOLA – **Namibe Province** • Iona NP (without precise locality); TM 40733–7; historical material • Road to Tambor; −15.8811, 012.2226; 186 m a.s.l.; PEM R17951.

Identification. A large (SVL 50–80 mm), rock-dwelling species that is associated with the arid Kaokoveld, characterised by presence of 2 or 3 weak keels on dorsal scales and 32 scale rows at midbody (Branch 1998).

Biology and distribution. It has previously been reported from Iona NP, from the Curoca River at the Pediva Hot Springs (Ceríaco et al. 2016a). The historical Ditsong Museum records collected from Iona NP lack accurate locality information but were presumably collected within the boundaries of the park. During this study we observed individuals in the mountains southwest of Espinheira and at Tchamalindi.

***Trachylepis laevis* (Boulenger, 1907)**
Figure 7K

Material examined. ANGOLA – **Namibe Province** • Rio Curoca; −16.3000, 012.4200; TM 40593; historical material • Serra Cafema; −17.1269, 012.5126; 2030 m a.s.l.; P1.131; GenBank: ON006727. Salondjamba; –16.3070, 012.4195; photographic record.

Identification. *Trachylepis laevis* (SVL 45–60 mm) is mainly distinguished by its blue colouration and dorsolaterally flattened body. The specimen from the highlands of Serra Cafema is genetically similar (0.7%) to an individual from northern Namibia near the Cunene River (GenBank accession: MK792015).

Biology and distribution. Commonly found in Namibe Province, although records of the species in the literature are relatively few and scattered (Marques et al. 2018). Ceríaco et al. (2016) reported a record from north of Tambor, some 20 km outside the limits of Iona NP. Individuals were usually observed basking on granitic boulders or moving rapidly between small cracks and crevices. We report on the first confirmed records from Iona NP and its immediate vicinity, including historical specimens collected from near the Curoca River and to Serra Cafema over 2000 m a.s.l.

***Trachylepis occidentalis* (Peters, 1867)**
Figure 7L

Material examined. ANGOLA – **Namibe Province** • Rio Curoca Mouth; −15.7300, 011.9200; TM 40401, TM 40402; historical material • Espinheira; −16.7885, 012.3584; 455 m a.s.l.; PEM R17979, PEM R17980, PEM

R20356 • Kondundo; −16.8788, 012.3720; 515 m a.s.l.; JLRZC0117; GenBank: ON006728.

Identification. This species is a large (SVL 70–90 mm), ground-dwelling skink, distinguished from *T. hoeschi* and *T. binotata* (the other two large *Trachylepis* from Iona NP), based on the lack of keeled dorsal scales and the distinct dorsal coloration of red-brown to olive-brown background and three pale brown stripes with dark brown margins (Branch 1998). This specimen differs by less than 1% (16S) from material from the Northern Cape Province, South Africa (GenBank accession: HQ180020).

Biology and distribution. This skink is widely distributed across Namibia, Botswana, and southern Angola (Branch 1998; Marques et al. 2018). We report the first records from Iona NP with five specimens collected from Espinheira, Kondundo and Curoca River mouth. One specimen (JLRZC0117) was captured at midday while basking on branches of an isolated *Senegalia* spp. in the central plains.

***Trachylepis punctulata* (Bocage, 1872)**
Figure 7M

Material examined. ANGOLA – **Namibe Province** • Foz do Cunene; −17.2600, 011.7900; TM 40671; historical material • Otchifengo River; −16.6900, 013.0100; TM 40773; historical material • Rio Curoca Mouth; −15.7300, 011.9200; TM 40395–40397; Historical material • Road to Omauha; −16.1843, 012.4189; 365 m a.s.l.; FKH 0781; GenBank: ON006729 • Tonombe; −17.0964, 012.3035; 615 m a.s.l.; FKH 0791; GenBank: ON006730 • 9 km S of camp at the Red Canyon; −15.8007, 012.1238; 63 m a.s.l.; PEM R17998 • Omauha Lodge; −15.8760, 012.2058; 190 m a.s.l.; TM 40399 • Espinheira; −16.7908, 012.3569; 457 m a.s.l.; PEM R18002, PEM R18003.

Identification. This is a medium-sized skink (SVL 41–51.5 mm) with five keels on dorsal scales. The specimens reported here were identified genetically and all have identical 16S haplotypes (Table S2), while differing less than 3% from material from Namibia (GenBank accession: MK792035) by Weinell et al. (2019).

Biology and distribution. This skink is widely distributed in the arid regions of southern Africa and southwestern Angola (Pietersen et al. 2021). In Angola, the species has been previously reported across Namibe Province (Marques et al. 2018) and is commonly found within Iona NP (Ceríaco et al. 2016a). Individuals were often observed moving between large granitic boulders (Fig. 1F) in the lowlands of the central plains. Specimen FKH 0781 presented a different dorsal pattern in comparison with other material examined.

***Trachylepis sulcata* (Peters, 1867)**
Figure 7N

Material examined. ANGOLA – **Namibe Province** • Otchifengo River; −16.6900, 013.0100; TM 40775, TM 40776; historical material • Espinheira; −16.7885, 012.6127; 455 m a.s.l.; PEM R17975 • Tchamalindi; −16.9757, 012.8856; 1436 m a.s.l.; P1.97–8; GenBank: ON006731, ON006732.

Identification. This species is a medium-sized (SVL 65–75 mm), rupicolous skink that can be easily distinguished from its Angolan congeners based on its characteristic coloration with sexual dichromatism, wherein females present a markedly striped dorsal pattern and males are mostly dark brown and lack stripes. Recently, Butler (2020) recognised both *T. sulcata* (Namibian and South African populations) and *T. ansorgii* (from central Angola) as full species, provisionally allocating southwestern Angolan populations to *T. sulcata*, although the nuclear sequences show some similarity to *T. ansorgii*. Genetically the specimens from within Iona NP show little differentiation (1.61%, Table S2) and differ by 3.1% from specimens of *T. sulcata* collected in Namibia (GenBank accession: MK792054) and 3.4% to specimens assigned to *T. ansorgii* from Angola (GenBank accession: MK792055). This result agrees with that of Butler (2020) and shows a need for further investigation on this group.

Biology and distribution. *Trachylepis sulcata* is distributed from South Africa to southern Angola (Branch 1998). Individuals have been previously reported from Pediva Hot Springs in Iona NP (Ceríaco et al. 2016a). Here, we report the species as frequently observed in the surroundings of Iona NP amongst the large granitic boulders of Omauha Lodge. Two additional specimens were collected at Tchamalindi, above 1400 m a.s.l, and another was collected at Espinheira.

***Trachylepis* sp.**
Figure 7O

Material examined. ANGOLA – **Namibe Province** • Tchamalindi; −16.9757, 012.8856; 1436 m a.s.l.; FKH 0571, P1.102; GenBank: ON006733.

Identification. One specimen collected at the Cunene River, some 25 km west of Ruacana border post (PEM R17978; W. Conradie unpubl. data 2021) morphologically conforms to *T. variegata* based on the presence of three keels on the dorsal scales (Branch 1998). More recently, two specimens were collected at Tchamalindi Mountain, which morphologically also resemble with *T. variegata*. However, sequence divergence shows that the Iona NP specimens differ more than 6% from a specimen collected from Savanna Guest Farm, Namibia (GenBank accession: MK792057) and cluster as a separate clade within the *variegata*-group. More comprehensive phylogenetic and morphological analysis are needed to resolve the status of these individuals.

Biology and distribution. This species was found during the day under the rocks at Tchamalindi Mountain.

Lacertidae

***Meroles anchietae* (Bocage, 1867)**
Figure 7P

Material examined. ANGOLA – **Namibe Province** • Foz do Cunene; −17.2600, 011.7900; TM 40643, TM 40644, TM 40710; historical material • Tòmbwa; −15.8200, 011.8800; TM 22574–22577, TM 24035–24039; historical material • Tchitchaki Valley; −16.3111, 012.2731; 236 m a.s.l.; FKH 0352 • 25 km NE from Foz de Cunene; −17.0967, 011.9167; 338 m a.s.l.; PEM R01793.

Identification. *Meroles anchietae* is a small lacertid (SVL 45–50 mm), easily identified based on its modified rostral scales and its bright yellow coloration (Branch 1998).

Biology and distribution. This sand-diving lacertid is adapted for living in the dunes of the Namib Desert (Edwards et al. 2016). While it was originally described from Angola (Bocage 1867), only a few records are known from the country to date while it is more commonly recorded from Namibia. We report it to be abundant at Iona NP from across the sand sea ecological zone, but fewer in smaller dunes of the coastal desert, where its sister species, *M. reticulatus*, is frequently recorded. *Meroles anchietae* is commonly found at the dune slip face, where the sand is much looser and easier to dive into. This species was observed in syntopy with *Gerrhosaurus skoogi*.

***Meroles reticulatus* (Bocage, 1867)**
Figure 7Q

Material examined. ANGOLA – **Namibe Province** • Curoca River Mouth; −15.7300, 011.9200; TM 40403–40414; Historical material • Tômbwa; −15.8200, 11.8800; TM 24030–24034; historical material • Foz do Cunene; −17.2638, 011.7950; 10 m a.s.l.; TM 40640–40642, TM 40669, TM 40709, FKH 0830, FKH 0516 • 25 km NE from Foz de Cunene; −17.0959, 011.9222; 345 m a.s.l.; PEM R17938.

Identification. *Meroles reticulatus* (SVL 45–50 mm) is the sister species of *M. anchietae* (Lamb and Bauer 2003; Edwards et al. 2016) and although described from Angola in the 19th century, very few country records have been published since. In the field, this species can be differentiated from *M. anchietae* by the presence of grey to blue-grey mottling with paler and darker grey tones dorsally and a less modified rostral scale (Branch 1998).

Biology and distribution. This species has been documented to occur on the gravel plains of the Namib Desert in southwestern Angola and northern Namibia (Marques et al. 2018), and in both sparsely vegetated loose sands and on harder packed soils of Namibia (Edwards et al. 2016). However, we only recorded the species in small, vegetated dunes in coastal areas where individuals move between small patches of vegetation. These lizards run fast and readily dive into loose sand when there is insufficient low vegetation to hide beneath. All specimens collected or photographed were observed during the day either near Tômbwa or Foz do Cunene localities where they seem to be quite common.

***Pedioplanis haackei* Conradie, Measey, Branch & Tolley, 2012**
Figure 7R

Material examined. ANGOLA – **Namibe Province** • Morro da Ilusão; −16.9353, 012.2489; 599 m a.s.l.; JL-RZC0119 • Along road to Tambor; −15.8761, 012.2058; 190 m a.s.l.; PEM R18465–R18467 • Dry riverbed in the road to Tambor; −15.8812, 012.2227; 185 m a.s.l.; PEM R18469; GenBank: HE793995 • Omauha Lodge; −15.9969, 012.4069; 301 m a.s.l.; PEM R18473 • Road to Espinheira; −15.9136, 012.3953; 317 m a.s.l.; PEM R18539.

Identification. This species (SVL 31.7–59.3 mm) may be morphologically distinguished from its Iona congeners based on its typical colouration of three pale dorsolateral stripes becoming faint posteriorly versus five dark grey ventral lines with clear white borders posteriorly in *Pedioplanis huntleyi* and dorsolateral stripes, often broken, and vertebral stripe indistinct in *P. serodioi*. Our collected specimen is genetically similar to existing material (0.94%, Table S2).

Biology and distribution. This is an Angolan endemic, restricted to the southwest of the country. It usually occurs in semi-arid shrubland on sandy substrates with low vegetation. Previously reported from the northern and central regions of Iona NP (Conradie et al. 2012; Parrinha et al. 2021), but we also recorded a specimen (JL-RZC0119) (Fig. 2I) from ~40 km south of Espinheira. This record represents the southernmost record for the species, revealing a wide distribution in the park including the consolidated dunes towards the Cunene River.

***Pedioplanis huntleyi* Conradie, Measey, Branch & Tolley, 2012**
Figure 7S

Material examined. ANGOLA – **Namibe Province** • Tonombe; −17.0964, 012.3035; 615 m a.s.l.; FKH 0790; GenBank: ON006734 • Humbi; −16.9853, 012.5420; 871 m a.s.l.; FKH 0799; GenBank: ON006735 • 40 km S of Omauha lodge; −16.5116, 012.4476; 369 m a.s.l.; PEM R18476 • Road to Oncócua; −16.8583, 012.6127; 808 m a.s.l.; PEM R18477–R18479; GenBank: HE794005 • Tchamalindi; −16.9754, 012.8858; 1434 m a.s.l.; FKH 0569 GenBank: ON006736 • 8 km NE of Iona; −16.8292, 012.6211; 741 m a.s.l.; PEM R18484; GenBank: HE794006 • 16 km E of Iona; −16.7981, 012.6806; 785 m a.s.l.; PEM R18485, PEM R18480; GenBank: HE794003 • 26 km E of Iona; −16.7006, 012.8242; 625 m a.s.l.; PEM R18486 • 14 km W of Moimba; −16.6794, 012.9739; 688 m a.s.l.; PEM R18481 • Helola; −16.6744, 012.8850; 603 m a.s.l.; PEM R18482.

Identification. *Pedioplanis huntleyi* is medium-sized lacertid (SVL 47.5–58.9 mm). See the description of *P. haackei* for its morphological characterisation. The 16S sequence divergence values suggest there is structure among specimens collected within Iona NP (Table S2), possibly pointing to isolation between populations.

Biology and distribution. Endemic to Angola, is widely distributed in well-vegetated and compacted substrates in Namibe and Cunene provinces (Conradie et al. 2012; Parrinha et al. 2021).

***Pedioplanis serodioi* Parrinha, Marques, Heinicke, Khalid, Parker, Tolley, Childers, Conradie, Bauer & Ceríaco, 2021**
Figure 7T

Material examined. ANGOLA – **Namibe Province** • Mulola Humbi; −16.9411, 012.9203; 1299 m a.s.l.; FKH 0794, FKH 0795; GenBank: ON006737.

Identification. In a recent revision of the Angolan species of *Pedioplanis* a neotype was designated for *P. benguelensis* to stabilize the taxonomy (Parrinha et al. 2021). Rather than following Boulenger's (1919) diagnosis of a single transparent lower eyelid, Parrinha et al. (2021) stated that the colour description better matches the coastal population near the original type locality, with two transparent windows in the lower eyelid. All historical material having a single transparent window in the lower eyelid were transferred to a newly described species, *P. serodioi* (SVL 25–50.2 mm). Genetically this specimen fully agrees genetically with material previously assigned to *P. benguelensis* (Conradie et al. 2012), now been transferred to *P. serodioi*.

Biology and distribution. The species is widely distributed from central Benguela to the northern borders of Iona NP, with only two isolated records previously reported in the northern edge of the park (Conradie et al. 2012; Parrinha et al. 2021). We add two specimens found in the heart of Iona NP near Humbi, representing the southernmost records for the species.

Varanidae

***Varanus albigularis angolensis* Schmitd, 1933**
Figure 4H

Material examined. ANGOLA – **Namibe Province** • Omauha Logde; −16.2006, 012.4018; 341 m a.s.l.; photographic record.

Identification. This species is the only terrestrial monitor found in the area. This species ia very large (SVL 400–500 mm), stout lizard has strong, stocky kimbs and sharp claws.

Biology and distribution. *Varanus albigularis* (SVL 400–500 mm) is widely distributed in Southern Africa. However, the subspecies *V. a. angolensis* has been considered to be only present in Angola. Records of this subspecies are rare and clearly opportunistic (Phillips 2004; Ceríaco et al. 2016a; Marques et al. 2018). We report on a specimen captured in Omauha Lodge, a private property on the northern border of the park. The species is regularly observed by the staff of Iona NP. Due to its broad distribution and the ease of identification, we consider these ad hoc records as valid and include it in the Iona NP species list.

***Varanus niloticus* (Linnaeus, 1758)**

Material examined. ANGOLA – **Namibe Province** • Foz do Cunene; −17.2600, 011.7900; TM 40664; historical material.

Identification. This species is the largest (SVL 600–800 mm) monitor lizard in Africa. It has a stout body with powerful limbs, strong claws, and an elongate snout. The tongue is dark, almost black. Tail long, laterally compressed, with a low dorsal crest. Limbs are spotted; the belly and throat are paler than dorsum, with black bars. Juvenile coloration is black and bright yellow.

Biology and distribution. This species is well adapted to live in deep river valleys in all Sub-Saharan countries from the Nile River in Egypt throughout the network of rivers across most of Africa, reaching southwest to Angola and Namibia (Wilms et al. 2021). The species was previously documented along the Cunene River (Cunningham et al. 2018) and one specimen was collected at Foz do Cunene in 1971, the only material known from Iona NP.

Viperidae

***Bitis arietans* (Merren, 1820)**
Figure 8A

Material examined. ANGOLA – **Namibe Province** • Tchamalindi; −16.9757, 012.8856; 1436 m a.s.l.; P1.113; GenBank: ON006738 • Vitambi; −17.0822, 012.2638; 548 m a.s.l.; photographic record.

Identification. This is a heavily built snake (SVL 1090–1100 mm) with large, flattened, triangular head and large nostrils oriented vertically upwards. In March 2021, a shed skin was collected at Tchamalindi and the DNA sequence of this skin was a positive match to *B. arietans*. This specimen matches *B. arietans* DNA sequence (<1%) from South Africa (GenBank accession: GQ359736). A second adult specimen was found active at night on a dry riverbed.

Biology and distribution. Assumed to be present across most of Angola, although there were no previous records from Iona NP, and only one doubtful record from Namibe Province (Branch 2018; Marques et al. 2018; Conradie et al. 2021). Nevertheless, park rangers claimed frequent observations of this snake, and it has been observed in coastal Namib Desert further south, for example at the Kuiseb Mouth, Walvis Bay (Stuart 1980). These records represent the only confirmed records of the species in Iona NP, spanning an elevational range from sea level to above 2000 m a.s.l.

***Bitis caudalis* (Smith, 1839)**
Figure 8B

Material examined. ANGOLA – **Namibe Province** • 50 km from Tômbwa; −15.8800, 012.2100; TM 40427–8; historical material • Tchitchaki Valley; −16.2850, 012.2815; 223 m a.s.l.; photographic record • Espinheira; −16.7886, 012.3584; 489 m a.s.l.; photographic record

Figure 8. Snakes from Iona National Park. **A.** *Bitis arietans*. **B.** *Bitis caudalis*. **C.** *Naja nigricincta*. **D.** *Python anchietae*. **E.** *Python natalensis*. **F.** *Lycophidion namibianum*. **G.** *Psammophis leightoni*. **H.** *Psammophis notostictus*. **I.** *Hemirhagerrhis viperina*. **J.** *Prosymna frontalis*. **K.** *Prosymna visseri*. **L.** *Pythonodipsas carinata*. **M.** *Namibiana* cf. *occidentalis*. Photographs by JLR (B, D, E, G, H, L), PVP (A, I, M), William R. Branch (F, J, K), and Ninda Baptista (C).

• Curoca River at Omauha Water Cistern; −16.2648, 012.3224; 185 m a.s.l.; photographic record.

Identification. This species is the only recorded species of dwarf adder in Angola (SVL 372–548 mm), characterized by the presence of the characteristic horn ornamentation or elongated supraorbital scales.

Biology and distribution. This species is widely distributed in southwestern Angola (Marques et al. 2018) in arid biomes (Branch 1998), and it was frequently encountered within Iona NP during our surveys. Individuals were recorded from Tchitchaki River, Curoca River, the central plains (near Espinheira), the sand sea zone, and southwestern Iona NP (Fig. 1A). These snakes where always recorded during the day, sheltering under dead welwitschias, basking close to rocks, or hidden under rocks. The observations were either opportunistic or by following their tracks in the sand.

Elapidae

***Naja nigricincta* Bogert, 1940**
Figure 8C

Material examined. ANGOLA – **Namibe Province** • Foz do Cunene; −17.2600, 011.7900; TM 39931; historical material • 2 km W of Iona Village; −16.8940, 012.5540; 726 m a.s.l.; photographic record.

Identification. *Naja nigricincta* is a large elapid (SVL 1470–2000 mm) originally described from southwestern Angola but synonomised with *N. nigricollis* Reinhardt, 1843 by Broadley (1974). It has subsequently been recognized as a separate species from *N. nigricollis* (Wüster & Broadley 2007).

Biology and distribution. Although not specifically recorded during our surveys (but see below), this snake is usually encountered during the day, moving in open areas or between rocks. However, most records derive from opportunistic visual observations without genetic or even photographic support. In Iona NP, the only available material was a single specimen collected in 1971 at Foz do Cunene (Broadley 1974). Despite not being recorded during our surveys, one team member (Bruce Bennet) was bitten at night by an individual at Espinheira in 2009. While that particular snake escaped in the

ensuing excitement and commotion, we suggest that this species is widespread in the park. Additionally, a photographic record of a roadkill was made in Iona NP (N. Baptista and T. Antonio; Fig. 8C).

***Dendroaspis polylepis* Günther, 1864**

Material examined. ANGOLA – **Namibe Province** • Serra Cafema; −17.1269, 012.5126; 1434 m a.s.l.; P1-121; GenBank: ON006739.

Identification. *Dendroaspis polylepis* is a large (SVL 2330 – 2530 mm), streamlined snake with a narrow, coffin-shaped head and smooth scales in 23–25 oblique rows. The DNA sequence retrieved from one shed skin matched other sequenced material of *Dendroaspis polylepis* (KA Tolley unpubl. data) with approximately 3% sequence divergence. The skin sample showed a comparatively higher divergence to other species of mamba in GenBank (approximately 6% divergence). Therefore, the shed skin is tentatively assigned to *D. polylepis*.

Biology and distribution. This species is widely distributed in the savanna of Sub-Saharan Africa (Branch et al. 2021). In Angola, the species has been reported from the plateau region, with no confirmed records from Namibe Province (Branch 2018; Marques et al. 2018; Conradie et al. 2021), even though a few records have been documented in semi-arid savanna, in coastal Hanha, Benguela Province (Bogert 1940). In March 2021, a shed snakeskin found near a granite outcrop was collected at Cafema Mountain. This record is the first of the species for Iona NP and represents the southernmost record in the country.

Pythonidae

***Python anchietae* Bocage, 1887**
Figure 8D

Material examined. ANGOLA – **Namibe Province** • Omauha Logde; −16.2006, 012.4018; 341 m a.s.l.; photographic record • Iona village; −16.8831, 012.5707; 754 m a.s.l.; photographic record.

Identification. This is a medium-sized to small, rock-dwelling python (SVL 1290–1520 mm), with five heat-sensitive labial pits. The body is pale red-brown with black-edged white spots and bands.

Biology and distribution. This species is mostly restricted to the coastal plain in southern Angola and more extensively distributed in northern Namibia (Branch 2018). It is usually found moving about at night. While this species has been assumed to be present in Iona NP (Marques et al. 2018), all known records were based on captive (wild caught from the area) specimens kept in Omauha Lodge, a private reserve adjacent to Iona NP. Here, we report on an additional individual photographed by Tchafeni Augusto near Iona village, which to our knowledge constitutes the first confirmed record in the park (N. Baptista and T. Antonio unpubl. data 2020).

***Python natalensis* (Gmelin, 1788)**
Figure 8E

Material examined. ANGOLA – **Namibe Province** • Omauha Logde; −16.2006, 012.4018; 341 m a.s.l.; photographic record.

Identification. *Python natalensis* (SVL 4.25–5 m) was previously recognized as a subspecies of *P. sebae*, and only recognized as a valid species in 1999, based on head scale variation and geographical distribution (Broadley 1999).

Biology and distribution. This species is a large and stout python usually found in open savanna and particularly rocky areas and riverine scrubs, and only absent from true desert and dense rain forest (Branch 1998). In Angola, the species is widely distributed in the southern half of the country (Marques et al. 2018; Conradie et al. 2021).

Lamprophiidae

***Lycophidion namibianum* Broadley, 1991**
Figure 8F

Material examined. ANGOLA – **Namibe Province** • Espinheira; −16.7886, 012.3584; 456 m a.s.l.; PEM R17995.

Identification. This is the only wolf snake recorded in the area (SVL 315–530 mm). The species was described by Broadley (1991) from west of Usakos, Karibib District, northern Namibia and included many Namibian specimens previously confused with Laurent's *L. hellmichi* (Broadley 1991).

Biology and distribution. This is a species well adapted to arid rocky regions. The specimen from Espinheira was first reported by Branch (2018) and it was morphologically ascribed to *L. namibianum* based on the diagnostic lack of contact between the first supralabial and postnasal (versus contact in *L. hellmichi*) (Broadley 1991). This is also the only known record from Angola, extending its known distribution range northwards by ~180 km (Branch 2018; Branch et al. 2019).

Psammophiidae

***Psammophis leightoni* (Boulenger, 1902)**
Figure 8G

Material examined. ANGOLA – **Namibe Province** • 15 km NE of Foz do Cunene; −17.1700, 011.8600; TM 40708; historical material • Foz do Cunene; −17.2600, 011.7900; TM 39933; historical material • Tchitchaki Valley; −16.2800, 012.2800; 262 m a.s.l.; FKH 0788, FKH 0789; GenBank: ON006740.

Identification. *Psammophis leightoni* (SVL 798–960 mm) is a slender snake with 17 scale rows, eight upper labials, and one preocular. The posterior nasal is divided, as is the anal. It was recently considered as a senior synonym of *P. namibensis* (Taft et al. 2021). A preliminary phylogenetic analysis with unpublished material from

Namibia (C. Keates unpubl. data 2021) cluster together with the Angolan material.

Biology and distribution. As a consequence of the re-evaluation of the species (Taft et al. 2021), this species now has a large known distribution in the western arid region from Angola to South Africa, being commonly found in dunes of the Namib Desert, moving actively during the day between small patches of vegetation (Branch 2018). The specimens reported here from Iona NP were always found during the day by following characteristic tracks visible in the soft sand of the desert dunes region (Fig. 2F). Two morphotypes have been identified in Angola, with three of our specimens displaying the typical three dorsal stripes and one specimen having one single dorsal stripe.

***Psammophis leopardinus* Bocage, 1887**

Material examined. ANGOLA – **Namibe Province** • Iona Natural Reserve (without precise locality): TM 40752; historical material.

Identification. This whip snake (maximum SVL 985 mm) can be distinguished from other Angolan whip-snakes by the head markings and spotted dorsal pattern with a yellow dotted vertebral line.

Biology and distribution. This species has been recorded from arid savanna and semi-desert regions in southern Angola and central Namibia (Marques et al. 2018), characterized by its characteristic dorsal pattern and arboreal behaivor (Vaz Pitnto et al. 2019). The specimen recorded from Iona NP was collected in 1971 and included in the revision of the genus by Broadley (2002). It constitutes the southernmost record for the species in Angola.

***Psammophis notostictus* Peters, 1867**

Figure 8H

Material examined. ANGOLA – **Namibe Province** • 60 km S of Moçamedes on road to Tômbwa; −15.6979, 012.0837; 138 m a.s.l.; FKH 0783; GenBank: ON006741.

Identification. This species (SVL 680–733 mm) can be distinguished from *P. leightoni* based on the presence of two preocular scales and divided postcloacal scales (versus one preocular and undivided in *P. leightoni*). Preliminary phylogenetic analysis shows that the Angolan specimens differ genetically from the material of *P. notostictus* from South Africa (Keates 2021).

Biology and distribution. A slender sand snake that is widely distributed from South Africa to Angola and is frequently found in arid scrubland and gravel plains (Branch 1998). The species has been recorded within Iona NP (Ceríaco et al. 2016a) and an additional specimen was collected during our surveys on the road between Tômbwa and Moçamedes, relatively close to the northwestern border of Iona NP.

***Psammophis trigrammus* Günther, 1865**

Material examined. ANGOLA – **Namibe Province** • Rio Curoca; −16.3000, 012.4200; TM 40540; historical material.

Identification. This is a very slender and fast-moving snake, frequently recorded from arid scrubland, hunting skinks and lacertids during the heat of the day (Branch 1998). Specimens collected in 1971 in Iona NP or its vicinity were included in the revision of the genus by Broadley (2002) and correspond to the southernmost records for the species in Angola.

***Hemirhagerrhis viperina* (Bocage, 1873)**

Figure 8I

Material examined. ANGOLA – **Namibe Province** • Tchamalindi; −16.9768, 012.8782; 1434 m a.s.l.; P1-116; GenBank: ON006742.

Identification. *Hemirhagerrhis viperina* is a small (SVL 270–295 mm), slender snake that may be distinguished from other lamprophiids by its flattened and slender body and dark brown or black triangular markings on the dorsum (Branch 1998). DNA barcoding shows that this individual is similar to samples collected from other regions of Namibe Province (Lobon-Rovira unpubl. data 2021).

Biology and distribution. This lamprophiid snake has been often recorded from southwestern Angola and northern Namibia, living between cracks and crevices in granitic boulders (Branch 1998). However, the species had not been reported previously from Iona NP or its surroundings (Marques et al. 2018). During our surveys, we recorded it from the highlands of Iona NP at Cafema and Tchamalindi mountains where it was frequently found during the day sheltering inside narrow cracks and under rock flakes. These records are the first for the species from Iona NP.

Prosymnidae

***Prosymna* cf. *frontalis* Peters, 1867**

Figure 8J

Material examined. ANGOLA – **Namibe Province** • Espinheira; −16.7886, 012.3584; 456 m a.s.l.; PEM R17997; GenBank: MT460615.

Identification. This is a small shovel-snout snake (SVL 290–380 mm). Bocage (1873) ascribed Angolan material from both the coast and inland to this species, but those specimens were subsequently re-evaluated by Boulenger (1915) and assigned to a new species, *P. angolensis*, based on lower number of subcaudal scales. However, recent phylogenetic analysis of the genus revealed two well-differentiated clades within *P. frontalis*, one from northern Namibia and Angola (including material listed here) and the other from central Namibia southwards to South Africa (Heinicke et al. 2020). More work is needed to resolve the taxonomic status of Angolan material.

Biology and distribution. This fossorial snake is restricted to the arid landscapes from southern Angola to the Northern Cape Province in South Africa (Broadley 1980). The species was described from Otjimbingue, Namibia (Peters, 1867).

***Prosymna visseri* FitzSimons, 1959**
Figure 8K

Material examined. ANGOLA – **Namibe Province** • Espinheira; −16.7886, 012.3584; 456 m a.s.l.; PEM R17994, PEM R17996; GenBank: MT460630.

Identification. This is a morphologically distinctive fossorial snake (SVL 263–310 mm) with marked cranial differences relative to closely related species (Heinicke et al. 2020). However, the specimens listed here, and first reported by Branch (1998), confirm the species occurrence in Iona NP and were included in a phylogenetic study where they clustered with additional material from Kunene region, Namibia (Heinicke et al. 2020).

Biology and distribution. The species was described from near Caraculo, Namibe Province (FitzSimons 1959) and is known to occur in Namibia extending further west inland (Bauer et al. 2000).

Pseudaspididae

***Pythonodipsas carinata* Günther, 1868**
Figure 8L

Material examined. ANGOLA – **Namibe Province** • Espinheira; −16.7856, 012.3589; 472 m a.s.l.; FKH 0818; GenBank: ON006743 • Vitambi; –17.0822, 012.2638; 548 m a.s.l.; photographic record.

Identification. *Pythonodipsas carinata* (SVL 515–770 mm) can be distinguished by its flattened head and large eyes with vertical pupils (Branch 1998). The collected specimen is similar (~2%) to material from Namibia (GenBank accession: AY188075).

Biology and distribution. This nocturnal snake is commonly found in the rocky desert of Namibia and southwestern Angola (Branch 1998). Nevertheless, Angolan published records are scarce and mostly without accurate locations (Branch et al. 1997). Here, we report on the first three records from Iona NP for a total of only seven records for Angola. The first indiviudal was observed on a rocky hill near Espinheira, the second was found in a dry river valley ~40 km south of Espinheira, and the third on a cliff along the Cunene River near Garota Nova. All the specimens were active at night moving amongst the rocks.

Leptotyphlopidae

***Namibiana* cf. *occidentalis* FitzSimons, 1962**
Figure 8M

Material examined. ANGOLA – **Namibe Province** • Pediva camp; −16.2173, 012.5167; 329 m a.s.l.; PEM R25091.

Identification. *Namibiana occidentalis* is a small (maximum SVL 322 mm), slender thread snake previously only known to occur in deserts and arid savannas from the Namibian Kaokoveld to northern Namaqualand in South Africa (Branch 1998). The species is morphologically diagnosable by the absence of the first anterior upper labial and the subvertical nasal suture (FitzSimons 1962).

Biology and distribution. Here, we report the first record of this species from Angola, collected just north of Pediva, near the northern border of Iona NP, thereby extending the known distribution to north of Cunene River. However, previous work from Namibia suggests that there is cryptic diversity within this group (Adalsteinsson et al. 2009). Due to lack of genetic evidence, we tentatively assign this species as *Namibiana* cf. *occidentalis* with the final identification awaiting further analyses.

Discussion

Over the last two decades, knowledge of Angolan herpetofauna has increased dramatically, and this has brought about new appreciation of the richness and diversity of the region (e.g., Cordylidae (Stanley et al. 2016; Marques et al. 2019b), Gekkonidae (Marques et al. 2021; Ceríaco et al. 2020a, 2020c; Branch et al. 2021; Lobon-Rovira et al. 2021), and Lacertidae (Conradie et al. 2012; Branch et al. 2029; Parrinha et al. 2021)). However, some herpetofaunal groups remain poorly documented and large areas of the country still lack comprehensive survey data (Branch et al. 2019; Huntley et al. 2019). This highlights the importance of compiling updated regional inventories (Conradie et al. 2016, 2021; Baptista et al. 2019b; Butler et al. 2019; Ernst et al. 2020). We provide here the first detailed inventory of the herpetofauna for Iona NP and report the occurrence of five amphibian and 70 reptile species. This study reports new records of 47 species for Iona NP and represents ~75% of all species known from Namibe Province (see Marques et al. 2018). We also report three species never before recorded in Angola (*Pachydactylus parascutatus*, *Namibiana* cf. *occidentalis*, and *Trachylepis* sp.), extend the known range of four endemic species (*Hemidactylus benguellensis*, *Cordylus namakuiyus*, *Lygodactylus nyaneka*, and *Panaspis mocamedensis*), and report on the occurrence of five undescribed species in the genera *Trachylepis* and *Pachydactylus*. We provide new insights into the biology of poorly known species (such as *Pachydactylus parascutatus*, *P. scutatus*, and *P. vanzyli*), and evidence of syntopy for several species (such as *Lygodactylus nyaneka* and *L. lawrencei*).

Iona National Park is one of the most geologically iconic and diverse areas in Angola with a panoply of geological formations, extending across four main ecological zones. The majority of Iona's herpetofauna are recognized as either psammophilic or rupicolous, with a few fossorial or arboreal species. Given the habitat and geological heterogeneity, we expected there to be an overall high species richness (e.g., Wiens 2004; Wollenberg Valero et al. 2019). Indeed, we found that the central plains are the most diverse region with 40 species recorded (57% of all species), followed by the mountainous region with 37 species recorded (representing 52%). Both regions have a large variety of soil and rock habitats. There are also 18 species more widely distributed,

occurring in both the mountainous regions and the central plains, with some species spanning an elevational range from sea level to above 2000 m a.s.l (e.g., *Kolekanos plumicaudus*, *Rhoptropus boultoni*, *Agama anchietae*, and *Bitis arietans*).

Nevertheless, we record several species with distributions that were restricted to only one of these ecological zones. For example, we recorded *Pedioplanis huntleyi* only in the eastern mountainous region, while its sister species *P. haackei* occurs extensively across the central plains. Our data suggests that the mountain ecological zone has the most species that occur only in one zone, despite it being the least explored due to its remoteness and poor accesibility. These results highlight the need for more extensive surveys to assess the biodiversity of the mountain zone and reinforces the importance of comprehensive biogeographic and phylogenetic studies to examine and assess the speciation process in this area more fully.

For many of the specimens collected, we used DNA barcoding to aid in identification to species level (e.g., Vences et al. 2012). Assessment of genetic sequences show that several species are comprised of complexes and show significant intraspecific diversity, and indicates the need for further work (e.g., *Pachydatylus oreophilus*, *P. punctatus*, *P.* cf. *vanzyli*, and *P.* cf. *rugosus*).

The number of snake species (16) reported is much lower than in other regions of Angola (Conradie et al. 2016, 2021; Baptista et al. 2019; Ernst et al. 2019) and neighbouring Namibia (Branch 1998). Some species, such as *Bitis peringueyi* (Boulenger 1888), that have never been reported in Angola (Branch 2018) may occur in Iona NP (Ceríaco et al. 2016a), because of the proximity of records in adjacent Namibia (Branch 1998). Despite several anecdotal observations of conspicuous sand tracks that might belong to this species (B. Bennet and B. Boon unpubl. data 2021), *B. peringueyi* has never been collected or photographed in Angola and it was not included in the list.

Other herpetofauna expected to be present, but not on our list, are the fossorial amphisbaenian lizards (Measey and Tolley 2013). Species of *Monopeltis* and *Zygaspis* are likely to occur in southwestern Angola and potentially inside Iona NP but are typically very cryptic and rarely encountered, even during targeted searches. Similarly, our species listed for Iona NP included a single scolecophidian snake, *Namibiana* cf. *occidentalis*, although we expect the area to include more members of the Leptotyphlopidae and Typhlopidae, which are also difficult to detect.

While some groups are under-represented in the comprehensive species list, we report a remarkable diversity of gekkonids in this region with 21 recognized species (+3 potentially new species within *P.* cf. *punctatus* and *P.* cf. *oreophilus* complexes). Our 21 geckos represent 36% of the recognized reptile diversity in the study area and over the 50% of all Angolan gekkonids. This diversity may be due to high heterogeneity of rocky substrates within Iona NP that may influence gekkonid diversification in the Namib region (Bauer 1999). Iona NP is part of the Namib desert biome, and neighboring Namibia contains 68 recognized gekkonids (Herrmann and Branch 2013). It is expected that additional surveys, phylogenetic analyses, and sophisticated species delimitation approaches will result in an increase in the number of gecko species for the whole region.

As a result of the recent surveys, Iona NP is now recognised as the most herpetologically species-rich conservation area in Angola (Conradie et al. 2016, 2021; Ceríaco et al. 2018b; Baptista et al. 2019a; Ernst et al. 2020) and may be a regionally important area. We believe that the number of species is underestimated, especially for snakes and fossorial species. Armed with improved knowledge, it is likely that conservation planning (e.g., Key Biodiversity Areas and/or Alliance for Zero Extinction sites) for Angola and for Iona NP will help to preserve a unique herpetofauna. This work could promote protection for some CITES protected species and other vulnerable species (e.g., *Kolekanos plumicaudus*).

Acknowledgements

We dedicate this work to two legendary African herpetologists, the late William R. Branch and Wulf Haacke. Both initiated early herpetological work in Angola and their collections not only made this work possible but will also fuel innumerable future works on the herpetofauna of Angola and southern Africa. This work was only possible due to the institutional collaboration with the Ministry of Culture, Tourism and Environment of the Republic of Angola (MCTA), and in particular, the support received by Dr. Albertina Nzuzi, Director of Instituto Nacional de Biodiversidade e Conservação (INBC), and previous partnership under the Ministry of Environment of the Republic of Angola (MINAMB). Material was collected under permits MINAMB 31/GGPCC/2016, ISCED/001/21. The biodiversity expedition of 2009 was funded by the National Research Foundation of South Africa and the South African National Biodiversity Institute. The mountain survey of 2021 was included in the SCIONA project, having received funding from the European Union under grant agreement FED/2017/394-802, and could not have been carried out without the hard work and organization ensured by Rolf Becker, Ansie Bosnam and Vera de Cauwer. Two additional surveys in 2021 were funded by The Wild Bird Trust through the Bill Branch Memorial Grant OWP015. A very special thanks to the owners of Omauha Lodge, Álvaro and Varito Baptista, for their generous logistical support, friendship and sharing of knowledge. We also thank Fernanda Lages and Vladimir Russo for coordinating institutional relationships and facilitating work authorizations. We especially thank Aaron Bauer in assisting with identifications and providing advice. We thank Ninda Baptista, Telmo Antonio, Octavio Mateus and Miguel Morais for providing useful photographs

of snakes, habitats, and sea turtles, respectively. JLR is currently supported by Fundação para a Ciência e Tecnologia (FCT) contract PD/BD/140808/2018. We also thanks to CTM workers (specially Susana and Rocio) at CIBIO for their tireless work and support in lab. Finally, we thank African Parks Iona, who entered into a 20-year partnership with the Angolan Government in 2020 and have provide infrastructure and field support for the latest expeditions. This work was supported by the European Union's Horizon 2020 Research and Innovation Programme under the Grant Agreement Number 857251.

Authors' Contributions

Conceptualization: PVP, JLR, WC. Data curation: JLR. Formal analysis: JLR. Funding acquisition: KAT, PVP. Investigation: WC, PVP, JLR. Methodology: JLR. Supervision: PVP, WC. Writing – original draft: JLR. Writing – review and editing: SS, WC, KAT, GJM, PVP, FSB, BBe, BBo.

References

Adalsteinsson SA, Branch WR, Trape S, Vitt LJ, Hedges SB (2009) Molecular phylogeny, classification, and biogeography of snakes of the Family Leptotyphlopidae (Reptilia, Squamata). Zootaxa 2244 (1): 1–50. https://doi.org/10.11646/zootaxa.2244.1.1

Andersson LG (1916) Notes on the reptiles and batrachians in the Zoological Museum at Gothenburg with an account of some new species. Göteborgs Kungliga Vetenskap och Vitter Hets-Samnalles Hndlingar Sjatte Foljden (Series B, 4) 17 (5): 1–41.

Altschul SF, Madden TL, Schäffer AA, Zhang J, Zhang Z, Miller W, Lipman DJ (1997) Gapped BLAST and PSI-BLAST: a new generation of protein database search programs. Nucleic Acids Research 25 (17): 3389–3402. https://doi.org/10.1093/nar/25.17.3389

Agarwal I, Ceríaco LMP, Bauer AM, Bandeira SA (2017) *Kolekanos plumicaudus* (Slender Feather-tailed Gecko) habitat use. Herpetological Review 48 (3): 649–650.

Baptista NL, António T, Branch WR (2019a) The herpetofauna of Bicuar National Park and surroundings, southwestern Angola: a preliminary checklist. Amphibian & Reptile Conservation 13 (2): 96–130.

Baptista N, Conradie W, Pinto PV, Branch WR (2019b) The amphibians of Angola: early studies and the current state of knowledge. In: Huntley BJ, Russo V, Lages F, Ferrand N (Eds). Biodiversity of Angola. Science & conservation: a modern synthesis. Springer Nature, Cham, Switzerland, 243–282. https://doi.org/10.1007/978-3-030-03083-4_13

Baptista NL, Tolley KA, Bluhm M, Finckh M, Branch WR (2020) Rediscovery, range extension, habitat and phylogenetic relation of the endemic Scaled Sandveld Lizard *Nucras scalaris* Laurent, 1964 (Sauria: Lacertidae) in the central Angolan plateau. African Journal of Herpetology 69 (1):12–28. https://doi.org/10.1080/21564574.2020.1778108

Baptista NL, Vaz Pinto P, Keates C, Edwards S, Roedel M-O, Conradie W (2021) A new species of red toad, Schismaderma Smith, 1849 (Anura: Bufonidae), from central Angola. Zootaxa 5081 (3): 301–332. https://doi.org/10.11646/zootaxa.5081.3.1

Bates MF, Bauer AM, Conradie W, Baptista N, Becker F, Ceríaco LMP (2020) *Pachydactylus rugosus*. The IUCN Red List of threatened species 2020. https://doi.org/10.2305/iucn.uk.2020-3.rlts.t196948a139766056.en. Accessed on: 2021-11-09.

Bates MF, Tolley KA, Edwards S, Davids Z, Da Silva JM, Branch WR (2013) A molecular phylogeny of the African plated lizards, genus *Gerrhosaurus* Wiegmann, 1828 (Squamata: Gerrhosauridae), with the description of two new genera. Zootaxa 3750 (5): 465–493. https://doi.org/10.11646/zootaxa.3750.5.3

Bauer A M (1999). Evolutionary scenarios in the *Pachydactylus* group geckos of southern Africa: new hypotheses. African Journal of Herpetology 48 (1–2): 53–62. https://doi.org/10.1080/21564574.1999.9651072

Bauer AM, Branch WR (2002) A revision of *Pachydactylus scutatus* (Reptilia: Squamata: Gekkonidae) with the description of a new species from norhtern Namibia. Proceedings of the California Academy of Sciences 53 (3): 23–36.

Bauer AM, Lamb T (2005) Phylogenetic relationships of southern African geckos in the *Pachydactylus* group (Squamata: Gekkonidae). African Journal of Herpetology 54 (2): 105–129.

Bauer AM, Lamb T, Branch WR (2002) A revision of *Pachydactylus scutatus* (Reptilia: Squamata: Gekkonidae) with the description of a new species from northern Namibia. Proceedings of the California Academy of Sciences 53 (3): 23–36.

Bauer AM, Lamb T, Branch WR, Babb RD (2000) New records of two rare snakes from northern Namibia, with comments on the Trans-Kunene distribution of Mopaneveld squamates (Squamata: Serpentes: Colubridae). Herpetozoa 14 (1–2): 75–79.

Bittencourt-Silva GB (2019) A herpetological survey of western Zambia. Amphibian & Reptile Conservation 13 (2): 1–28.

Bocage JVB (1895) Herpétologie d'Angola et du Congo. Ministério da Marinha e das Colónia, Lisbonne, Portugal, 203 pp., 20 pls.

Bogert CM (1940) Herpetological results of the Vernay Angola Expedition. Bulletin American Museum of Natural History 77: 1–107.

Branch WR (1998) Field guide to snakes and other reptiles of Southern Africa. Struiks, Cape Town, South Africa, 399 pp.

Branch WR (2008) Tortoises terrapins and turtles of Africa. Struik Publishers, Cape Town, South Africa, 128 pp.

Branch WR (2018) Snakes of Angola: an annotated checklist. Amphibian & Reptile Conservation 12 (2): 41–82.

Branch WR, Baptista N, Keates C, Edwards S (2019a) Rediscovery, taxonomic status, and phylogenetic relationships of two rare and endemic snakes (Serpentes: Psammophiinae) from the southwestern Angolan plateau. Zootaxa 4590 (3): 342–366. https://doi.org/10.11646/zootaxa.4590.3.2

Branch WR, Conradie W, Vaz Pinto P, Tolley K (2019b) Another Angolan Namib endemic species: a new *Nucras* Gray, 1838 (Squamata: Lacertidae) from south-western Angola. Amphibian and Reptile Conservation 12 (2):85–95.

Branch WR, Trape JF, Luiselli L, Spawls S, Penner J, Howell K, Msuya CA, Ngalason W (2021) *Dendroaspis polylepis*. The IUCN Red List of threatened species 2021. https://doi.org/10.2305/iucn.uk.2021-2.rlts.t177584a15627370.en. Accessed on: 2021-11-09.

Branch WR, Vaz Pinto P, Baptista N, Conradie W (2019c) The reptiles of Angola: history, diversity, endemism and hotspots. In: Huntley B, Russo V, Lages F, Ferrand, N (Eds.) Biodiversity of Angola. Science & conservation: a modern synthesis. Springer, Cham, Switzerland, 283–334. https://doi.org/10.1007/978-3-030-03083-4_13

Branch WR, Conradie W (2013) *Naja annulata annulata* (Bucholtz & Peters, 1876). African Herp News 59: 50–53.

Branch WR, Haacke W, Vaz Pinto P, Conradie W, Baptista N, Verburgt L (2017) Loveridge's Angolan geckos, *Afroedura karroica bogerti* and *Pachydactylus scutatus angolensis* (Sauria, Gekkonidae): new distribution records, comments on type localities and taxonomic status. Zoosystematics & Evolution 93: 157–166. https://doi.org/10.3897/zse.93.10915

Branch, WR, Schmitz A, Lobón-Rovira J, Baptista NL, António T, Conradie W (2021) Rock island melody: a revision of the *Afroedura bogerti* Loveridge, 1944 group, with descriptions of four new endemic species from Angola. Zoosystematics and Evolution 97: 55–82. https://doi.org/10.3897/zse.97.57202

Branch WR, Shine R, Harlow PS, Webb JK (1997) Sexual dimorphism, diet and aspects of reproduction of the western keeled

snake, *Pythonodipsas carinata* (Serpentes: Colubridae). African Journal of Herpetology 46 (2): 89–97. https://doi.org/10.1080/21564574.1997.9649982

Broadley DG (1974) A review of the cobras of the *Naja nigricollis* complex in southwestern Africa (Serpentes, Elapidae). Cimbebasia 2A: 155–162.

Broadley DG (1975). A review of the *Mabuya lacertiformis* complex in southern Africa (Sauria: Scincidae). Arnoldia Rhodesia 7: 1–16.

Broadley DG (1980) A revision of the African snake genus *Prosymna* Gray (Colubridae). Occasional Papers of the National Museums and Monuments of Rhodesia. Series B, Natural Sciences 6: 481–556.

Broadley DG (1991) A review of the Namibian snakes of the genus *Lycophidion* (Serpentes: Colubridae), with the description of a new endemic species. Annals of the Transvaal Museum 35 (14): 209–215.

Broadley DG (1999) The southern African python, *Python natalensis* A. Smith 1840, is a valid species. African Herp News 29: 31–32

Butler BO (2020) Systematics and phylogeography of two southwest African lizard taxa. Master's thesis, Villanova University, Vilanova, PA, USA, 169 pp.

Butler BO, Ceríaco LMP, Marques MP, Bandeira S, Túlio T, Heinicke MP, Bauer AM (2019) Herpetological survey of Huíla Province, southwest Angola, including first records from Bicuar National Park. Herpetological Review 50 (2): 225–240.

Ceríaco LMP, Bauer AM, Blackburn DC, Lavres ACF (2014) The herpetofauna of the Capanda Dam Region, Malanje, Angola. Herpetological Review 45 (4):667–674

Ceríaco LMP, de Sá, SDAC, Bandeira S, Valério H, Stanley EL, Kuhn AL, Marques MP, Vindum JV, Blackbrun DC, Bauer AM (2016a) Herpetological survey of Iona National Park and Namibe Regional Natural Park, with a synoptic list of the amphibians and reptiles of Namibe Province, southwestern Angola. Proceedings of the California Academy of Sciences 63 (2): 15–61.

Ceríaco LMP, Bauer AM, Heinicke MP, Blackbrun DC (2016b) *Chondrodactylus pulitzerae* (Schmidt, 1933), Pulitzer's Thick-toed Gecko in Angola. African Herp News 64: 41–44.

Ceríaco LMP, Marques MP, Bandeira S, Agarwal I, Stanley EL, Bauer AM, Heinicke MP, Blackburn DC (2018a) A new earless species of *Poyntonophrynus* (Anura, Bufonidae) from the Serra da Neve Inselberg, Namibe Province, Angola. ZooKeys 780: 109–136. https://doi.org/10.3897/zookeys.780.25859

Ceríaco LMP, Marques MP, Bandeira S, Blackburn DC, Bauer AM (2018b) Herpetological survey of Cangandala National Park, with a synoptic list of the amphibians and reptiles of Malanje Province, Central Angola. Herpetological Review 49 (3): 408–431.

Ceríaco LMP, Agarwal I, Marques MP, Bauer AM (2020a) A review of the genus *Hemidactylus* Goldfuss, 1820 (Squamata: Gekkonidae) from Angola, with the description of two new species. Zootaxa 4746 (1):1–71. https://doi.org/10.11646/zootaxa.4746.1.1

Ceríaco LMP, Heinicke MP, Parker K, Marques MP, Bauer AM (2020b) A review of the African snake-eyed skinks (Scincidae: *Panaspis*) from Angola, with the description of a new species. Zootaxa 4747:77–112. https://doi.org/10.11646/zootaxa.4747.1.3

Ceríaco LMP, Agarwal I, Marques MP, Bauer AM (2020c) A correction to a recent review of the genus *Hemidactylus* Goldfuss, 1820 (Squamata: Gekkonidae) from Angola, with the description of two additional species. Zootaxa 4861 (1): 92–106. https://doi.org/10.11646/zootaxa.4861.1.6

Ceríaco LMP, Santos BS, Marques MP, Bauer AM, Tiutenko A (2021) Citizen science meets specimens in old formalin filled jars: a new species of banded rubber frog, genus *Phrynomantis* (Anura: Microhylidae) from Angola. Alytes 38 (1–4): 18–48.

Channing A, Becker F (2019) Correction to the type locality of *Tomopterna ahli* (Deckert, 1938) (Anura: Pyxicephalidae), with the designation of a neotype. Zootaxa 4688 (4): 6 https://doi.org/10.11646/zootaxa.4688.4.6

Channing A, Rödel MO (2019) Field guide to the frogs & other amphibians of Africa. Penguin Random House, Cape Town, South Africa, 408 pp.

Chippaux JP, Jackson K (2019) Snakes of central and western Africa. Johns Hopkins University Press, Baltimore, MD, USA, 448 pp.

Conradie W, Bills R, Branch WR (2016) The herpetofauna of the Cubango, Cuito, and lower Cuando river catchments of south-eastern Angola. Amphibian & Reptile Conservation 10 (2): 6–36.

Conradie W, Bourquin S (2013) Geographical distributions: *Acontias kgalagadi kgalagadi* (Lamb, Biswas and Bauer, 2010). African Herp News 60: 29–30.

Conradie W, Measey GJ, Branch WR, Tolley KA (2012b) Revised phylogeny of African sand lizards (*Pedioplanis*), with the description of two new species from south-western Angola. African Journal of Herpetology 61 (2): 91–112. https://doi.org/10.1080/21564574.2012.676079

Conradie W, Branch WR, Measey GJ, Tolley KA (2012a) A new species of *Hyperolius* Rapp, 1842 (Anura: Hyperoliidae) from the Serra da Chela mountains, southwestern Angola. Zootaxa 3269 (1): 1–17. https://doi.org/10.11646/zootaxa.3269.1.1

Conradie W, Branch WR, Tolley KA (2013) Fifty shades of grey: giving colour to the poorly known Angolan Ashy reed frog (Hyperoliidae: *Hyperolius cinereus*), with the description of a new species. Zootaxa 3635 (3): 201–223. https://doi.org/10.11646/zootaxa.3635.3.1

Conradie W, Deepak V, Keates C, Gower, DJ (2020b) Kissing cousins: a review of the African genus *Limnophis* Günther, 1865 (Colubridae: Natricinae), with the description of a new species from north-eastern Angola. African Journal of Herpetology 69 (1): 79–107. https://doi.org/10.1080/21564574.2020.1782483

Conradie W, Keates C, Lobón-Rovira J, Vaz Pinto P, Verburgt L, Baptista NL, Harvey J, Júlio T (2020a) New insights into the taxonomic status, distribution and natural history of De Witte's Clicking Frog (Kassinula wittei Laurent, 1940). African Zoology 55 (4): 311–322. https://doi.org/10.1080/15627020.2020.1821771

Conradie W, Baptista NL, Verburgt L, Keates C, Harvey J, Júlio T, Neef G (2021) Contributions to the herpetofauna of the Angolan Okavango-Cuando-Zambezi River drainages. Part 1: Serpentes (snakes). Amphibian & Reptile Conservation 15 (2): 244–278.

Cunningham PL, Maartens L, Prickett M (2018) A contribution to the reptiles of the Kunene River Mouth area. Namibian Journal of Environment 2: B-8.

Edwards S, Herrel A, Vanhooydonck B, Measey GJ, Tolley KA (2016) Diving in head first: Investigations into trade-offs between phenotypic traits and sand-diving predator escape strategy in desert lizards (Meroles, Lacertidae, Squamata). Biological Journal of the Linnean Society 119 (4): 919–931. https://doi.org/10.1111/bij.12856

Ernst R, Lautenschläger T, Branquima MF, Hölting M (2020) At the edge of extinction: a first herpetological assessment of the proposed Serra do Pingano Rainforest National Park in Uíge Province, northern Angola. Zoosystematics and Evolution 96: 237–262

Ernst R, Nienguesso ABT, Lautenschläger T, Barej MF, Schmitz A, Hölting M (2014) Relicts of a forested past: Southernmost distribution of the hairy frog genus *Trichobatrachus* Boulenger, 1900 (Anura: Arthroleptidae) in the Serra do Pingano region of Angola with comments on its taxonomic status. Zootaxa 3779: 297–300. https://doi.org/10.11646/zootaxa.3779.2.10

Ernst R, Schmitz A, Wagner P, Branquima MF, Hölting M (2015) A window to Central African forest history: distribution of the *Xenopus fraseri* subgroup south of the Congo Basin, including arst country record of *Xenopus andrei* from Angola. Salamandra 51: 147–155.

Faith DP, Walker PA (2002) The role of trade-offs in biodiversity conservation planning: linking local management, regional planning and global conservation efforts. Journal of Biosciences 27 (4): 393-407.

FitzSimons VFM (1962) Snakes of Southern Africa. Purnell, Cape Town, South Africa, 423 pp.

Griffin M, Channing A (1991) Wetland associated reptiles and amphib-

ians of Namibia—a national review. Madoqua 17 (2): 221–225.

Haacke WD (2008) A new leaftoed gecko (Reptilia: Gekkonidae) from south-western Angola. African Journal of Herpetology 57 (2): 85–92.

Haacke WD (1976) The burrowing geckos of southern Africa, 2 (Reptilia: Gekkonidae). Annals of the Transvaal Museum 30 (2): 13–28.

Haacke WD (1997) Systematics and biogeography of the southern African scincine genus *Typhlacontias* (Reptilia: Scincidae). Bonner Zoologische Beitrage 47: 139–164.

Hallermann J, Ceríaco LMP, Schmitz A, Ernst R, Conradie W, Verburgt L, Marques MP, Bauer AM (2020) A review of the Angolan House snakes, genus *Boaedon* Duméril, Bibron and Duméril (1854) (Serpentes: Lamprophiidae), with description of three new species in the *Boaedon fuliginosus* (Boie, 1827) species complex. African Journal of Herpetology 69 (1): 29–78. https://doi.org/10.1080/21564574.2020.1777470

Spotila JR (2004) Sea turtles: a complete guide to their biology, behavior, and conservation. Johns Hopkins University Press, MD, USA, 227 pp.

Heinicke MP, Adderly LM, Bauer AM, Jackman TR (2011) A long-known new species of gecko allied to *Pachydactylus bicolor* (Squamata: Gekkonidae) from the central Namibian coast. African Journal of Herpetology 60 (2): 113–129.

Heinicke MP, Ceríaco LMP, Moore IM, Bauer AM, Blackburn DC (2017) *Tomopterna damarensis* (Anura: Pyxicephalidae) is broadly distributed in Namibia and Angola. Salamandra 53 (3): 461–465.

Heinicke MP, Titus-McQuillan JE, Daza JD, Kull EM, Stanley EL, Bauer, AM (2020) Phylogeny and evolution of unique skull morphologies in dietary specialist African shovel-snouted snakes (Lamprophiidae: *Prosymna*). Biological Journal of the Linnean Society 131 (1): 136–153.

Heinz HM (2011) Comparative phylogeography of two widespread geckos from the typical narrow-ranging *Pachydactylus* group in Southern Africa. PhD Thesis, Villanova University, Villanova, PA, USA, 108pp.

Heinz MD, Brennan IG, Jackman TR, Bauer AM (2021) Phylogeny of the genus Chondrodactylus (Squamata: Gekkonidae) with the establishment of a stable taxonomy. Bulletin of the Museum of Comparative Zoology 163 (5): 151–210. https://doi.org/10.3099/0027-4100-163.5.151

Hellmich W (1957) Herpetologische Ergebnisse einer Forschungsreise in Angola. Veröffentlichugen der Zoologischen Staatssammlung München 5:1–92.

Herrmann HW, Branch WR (2013) Fifty years of herpetological research in the Namib Desert and Namibia with an updated and annotated species checklist. Journal of Arid Environments 93: 94–115. https://doi.org/10.1016/j.jaridenv.2012.05.003

Huntley B (2019) Angola in outline: physiography, climate and patterns of biodiversity. In: Huntley B, Russo V, Lages F, Ferrand N (Eds.) Biodiversity of Angola. Science & conservation: a modern synthesis. Springer, Cham, 283–334. https://doi.org/10.1007/978-3-030-03083-4_13

Huntley BJ, Ferrand N (2019) Angolan biodiversity: towards a modern synthesis. In: Huntley B, Russo V, Lages F, Ferrand N (Eds.) Biodiversity of Angola. science & conservation: a modern synthesis. Springer, Cham, Switzerland, 3–14. https://doi.org/10.1007/978-3-030-03083-4_13

Keates C (2021) Integrative systematic structuring of the widespread psammophiid snakes (Psammophiidae): a multi-evidence species delineation approach. PhD thesis, Rhodes University, Grahamstown, South Africa, 214 pp.

Kuhn A (2016) Systematics of the Namib day geckos (Squamata: Gekkonidae: Rhoptropus). Master's thesis, Villanova University, Villanova, PA, USA, 226 pp.

Lamb T, Bauer AM (2000) Relationships of the *Pachydactylus rugosus* group of geckos (Reptilia: Squamata: Gekkonidae). African Zoology 35 (1): 55–67. https://doi.org/10.1080/15627020.2000.11407192

Lamb T, Bauer AM (2003) *Meroles* revisited: complementary systematic inference from additional mitochondrial genes and complete taxon sampling of southern Africa's desert lizards. Molecular Phylogenetics and Evolution 29 (2): 360–364.

Lobón-Rovira J, Conradie W, Buckley Iglesias D, Ernst R, Veríssimo L, Baptista N, Vaz Pinto P (2021) Between sand, rocks and branches: an integrative taxonomic revision of Angolan *Hemidactylus* Goldfuss, 1820, with description of four new species. Vertebrate Zoology 71: 465–501. https://doi.org/10.3897/vz.73.e64781

Marques MP, Ceríaco LMP, Blackburn DC, Bauer AM (2018) Diversity and distribution of the amphibians and terrestrial reptiles of Angola—atlas of historical and bibliographic records (1840–2017). Proceedings of the California Academy of Sciences (Series 4) 65 (2): 1–501.

Marques MP, Ceríaco LMP, Bandeira S, Pauwels OSG, Bauer AM (2019a) Description of a new long-tailed skink (Scincidae: *Trachylepis*) from Angola and the Democratic Republic of Congo. Zootaxa 4568 (1): 51–68. https://doi.org/10.11646/zootaxa.4568.1.3

Marques MP, Ceríaco LM, Stanley EL, Bandeira SA, Agarwal I, Bauer AM (2019b) A new species of Girdled Lizard (Squamata: Cordylidae) from the Serra da Neve Inselberg, Namibe Province, southwestern Angola. Zootaxa 4668 (4): 503–524. https://doi.org/10.11646/zootaxa.4668.4.4

Marques MP, Ceríaco LMP, Buehler MD, Bandeira S, Janota JM, Bauer AM (2020) A revision of the dwarf geckos, genus *Lygodactylus* (Squamata: Gekkonidae), from Angola, with the description of three new species. Zootaxa 4583 (3): 301–352. https://doi.org/10.1093/sysbio/43.3.387

Marques MP, Parrinha D, Santos BS, Bandeira S, Butler BO, Sousa ACA, Bauer AM, Wagner P (2022) All in all it's just another branch in the tree: a new species of *Acanthocercus* Fitzinger, 1843 (Squamata: Agamidae), from Angola. Zootaxa 5099 (2): 221–243. https://doi.org/10.11646/zootaxa.5099.2.4

Mason N, Ward M, Watson JEM, Venter O, Runting RK (2020) Global opportunities and challenges for transboundary conservation. Nature Ecology & Evolution 4 (5): 694–701. https://doi.org/10.1038/s41559-020-1160-3

McLachlan GR, Spence JM (1967) A new species of *Pachydactylus* (*Pachydactylus oreophilus* sp. nov.) from Sesfontein, South West Africa. Cimbebasia 21: 3–8.

Measey GJ, Tolley KA (2013) A molecular phylogeny for sub-Saharan amphisbaenians. African Journal of Herpetology 62: 100–109. https://doi.org/10.1080/21564574.2013.824927

Monrad A (1937) Contribution à l'herpétologie d'Angola. Archivos do Museu Bocage 8: 19–154.

Morais M (2021) Projecto Kitabanga. Relatório de actividades e resultados 2020/2021. Unpublished progress report, Universidade Agostinho Neto, Luanda, Angola, 38 pp.

Nielsen SV, Conradie W, Ceríaco LMP, Bauer AM, Heinicke MP, Stanley EL, Blackburn DC (2020) A new species of rain frog (Brevicipitidae, *Breviceps*) endemic to Angola. ZooKeys 979: 133–160. https://doi.org/10.3897/zookeys.979.56863

Parrinha D, Marques MP, Heinicke MP, Khalid F, Parker KL, Tolley KA, Childers JL, Conradie W, Bauer AM, Ceríaco LM (2021) A revision of Angolan species in the genus *Pedioplanis* Fitzinger (Squamata: Lacertidae), with the description of a new species. Zootaxa 5032 (1): 1–46. https://doi.org/10.11646/zootaxa.5032.1.1

Palumbi SR, Martin AP, Romano SL, McMillan WO, Stice L, Grabowski G (1991) The simple fool's guide to PCR. Department of Zoology, University of Hawaii, Honolulu, USA, 45 pp.

Phillips JA (2004) *Varanus albigularis*. In: Pianka ER, King DR, King RA (Eds.) Varanoid lizards of the world. Indiana University Press, Bloomington/Indianopolis, USA, 608 pp.

Pietersen D, Verburgt L, Farooq H, Chapeta Y (2021) *Trachylepis punctulata*. The IUCN Red List of threatened species 2021. https://doi.org/10.2305/iucn.uk.2021-2.rlts.t110230238a147706253.en. Accessed on: 2021-11-09.

Poynton JC, Haacke W (1993) On a collection of amphibians from Angola, including a new species of *Bufo* Laurenti. Annals of the Transvaal Museum 36 (2): 9–16.

Prötzel D, Heß M, Schwager M, Glaw F, Scherz MD (2021) Neon-green fluorescence in the desert gecko *Pachydactylus rangei* caused by iridophores. Scientific Reports 11 (1): 1–10.

Rhodin AGJ, Iverson JB, Bour R, Fritz U, Georges A, Shaffer HB, van Dijk PP (2017) Turtles of the world: annotated checklist and atlas of taxonomy, synonymy, distribution, and conservation status. In: Rhodin AGJ, Iverson JB, van Dijk PP, Saumure RA, Buhlmann KA, Pritchard PCH, Mittermeier RA (Eds.) Conservation biology of freshwater turtles and tortoises: a compilation project of the IUCN/SSC Tortoise and Freshwater Turtle Specialist Group. Chelonian Research Monographs 7: 1–292. https://doi.org/10.3854/crm.7.checklist.atlas.v8.2017

Salerno J, Andersson K, Bailey KM, Hilton T, Mwaviko KK, Simon ID, Bracebridge C, Mangewa LJ, Nicholas A, Rutabanzibwa H, Hartter J (2021) More robust local governance suggests positive effects of long-term community conservation. Conservation Science and Practice 3: e297. https://doi.org/10.1111/csp2.297

Schmidt KP (1933) The reptiles of the Pulitzer-Angola Expedition. Annals of the Carnegie Museum 22: 1–15.

Sigovini M, Keppel E, Tagliapietra D (2016) Open nomenclature in the biodiversity era. Methods in Ecology and Evolution 7 (10): 1217–1225.

Simmons RE, Braby R, Braby SJ (1993) Ecological studies of the Cunene River mouth: avifauna, herpetofauna, water quality, flow rates, geomorphology and implications of the Epupa Dam. Madoqua 18 (2): 163–180.

Stanley EL, Ceríaco LM, Bandeira S, Valerio H, Bates MF, Branch WR (2016) A review of *Cordylus machadoi* (Squamata: Cordylidae) in southwestern Angola, with the description of a new species from the Pro-Namib desert. Zootaxa 4061 (3): 201–226. https://doi.org/10.11646/zootaxa.4061.3.1

Stuart CT (1980) An annotated preliminary list of amphibians and reptiles known to occur in the Namib Desert Park, Namibia. The Journal of the Herpetological Association of Africa 24 (1): 4–13.

Taft JM, Maritz B, Tolley KA (2021) Stable climate corridors promote gene flow in the Cape sand snake species complex (Psammophiidae). Zoologica Scripta. https://doi.org/10.1111/zsc.12514

Tilbury C (2018) Chameleons of Africa. Chimaira, Frankfurt am Main, Germany, 643 pp.

Vaz Pinto P, Veríssimo L, Branch WR (2019) Hiding in the bushes for 110 years: rediscovery of an iconic Angolan gecko (*Afrogecko ansorgii* Boulenger, 1907, Sauria: Gekkonidae). Amphibian & Reptile Conservation 13 (2): 29–41.

Vaz Pinto P, Conradie W, Becker F, Lobón-Rovira J (2021) Updated distribution of *Kolekanus plumicaudus* (Sauria: Gekkonidae), with some annotation on its natural history. Herpetology Notes 14: 1207–1212.

Vences M, Nagy ZT, Sonet G, Verheyen E (2012) DNA barcoding amphibians and reptiles. In: Kress W, Erickson D (Eds.) DNA barcodes: methods in molecular biology (methods and protocols). Humana Press, Totowa, USA, 9–108.

Wagner P. Butler BO, Ceriaco, LMP, Bauer AM (2021) A new species of the *Acanthocercus atricollis* complex (Squamata: Agamidae). Salamandra 57 (4): 449–463.

Weinell JL, Branch WR, Colston TJ, Jackman TR, Kuhn A, Conradie W, Bauer AM (2019) A species-level phylogeny of *Trachylepis* (Scincidae: Mabuyinae) provides insight into their reproductive mode evolution. Molecular Phylogenetics and Evolution 136: 183–195. https://doi.org/10.1016/j.ympev.2019.04.002

Wiens JJ (2004) What is speciation and how should we study it? The American Naturalist 163 (6): 914–23.

Wilms T, Wagner P, Luiselli L, Branch WR, Penner J, Baha El Din S, Beraduccii J, Msuya CA, Howell K, Ngalason W (2021) *Varanus niloticus*. The IUCN Red List of threatened species 2021. https://doi.org/10.2305/iucn.uk.2021-2.rlts.t198539a2531945.en. Accessed on: 2021-11-09.

Wollenberg Valero KC, Marshall JC, Bastiaans E, Caccone A, Camargo A, Morando M, Niemiller ML, Pabijan M, Russello MA, Sinervo B, Werneck FP, Sites JW Jr., Wiens JJ, Steinfartz S (2019) Patterns, mechanisms and genetics of speciation in reptiles and amphibians. Genes 10 (9): 646.

Wüster W, Broadley DG (2007). Get an eyeful of this: a new species of giant spitting cobra from eastern and north-eastern Africa (Squamata: Serpentes: Elapidae: *Naja*). Zootaxa 1532 (1): 51–68. https://doi.org/10.11646/zootaxa.1532.1.4

Zimkus BM, Rödel MO, Hillers A (2010) Complex patterns of continental speciation: molecular phylogenetics and biogeography of sub-Saharan puddle frogs (*Phrynobatrachus*). Molecular Phylogenetics and Evolution 55 (3): 883–900. https://doi.org/10.1016/j.ympev.2009.12.012